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THE GENUS *GOPHERUS* (TESTUDINIDAE):

PT. I. OSTEOLOGY AND RELATIONSHIPS OF EXTANT SPECIES

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GAINESVILLE

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THE GENUS *GOPHERUS* (TESTUDINIDAE):
PT. I. OSTEOLOGY AND RELATIONSHIPS OF EXTANT SPECIES

WALTER AUFFENBERG¹

SYNOPSIS: Adult skeletons of the extant species of the genus *Gopherus* were studied to determine the kind and level of similarities and differences between them and to form a comparative base for studies of fossil members of the genus. The skeleton and its variation in each of the species is described and/or figured and analyzed. The four extant species form two species groups, based on a number of osteological characters. One group includes *G. polyphemus* and *G. flavomarginatus*; the other *G. berlandieri* and *G. agassizi*. *G. polyphemus* and *berlandieri* represent the morphological extremes of each group. *G. flavomarginatus* and *agassizi* overlap in a number of characters, and may be close to the evolutionary base of both groups.

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INTRODUCTION

The present osteological study of extant populations of the genus *Gopherus* is the first of several intended to treat both Recent and fossil populations. It has two purposes: (1) to determine the systematic relations of these populations to one another, and (2) as a basis of comparison for studies of the earlier fossil members of the genus.

The earliest known geologic occurrence of the genus is in Lower Oligocene rocks of the White River Formation in Colorado, Nebraska, Wyoming, and South Dakota (*Gopherus laticunae* and *Gopherus praextans*). From that period to the present the fossil history is unbroken, although the relationships of the extinct populations to one another are not clear. What is certain, however, is that the genus *Gopherus* is closely related to the extinct genus *Stylemys*. This is based on certain features of the shell and skull (Williams 1950a; Hay 1908). The most important correlative character is the presence of a median premaxillary ridge, which is found only in these two genera of land tortoises. The presumed phalangeal differences between these genera mentioned by several earlier workers has been shown to be incorrect (Auffenberg 1961). However, certain differences in rate of shell ossification during ontogenetic development and the shape of particular parts of the skeleton in adults seem sufficiently great to consider these two related phyletic lines distinct at

the generic level (Auffenberg 1963), at least since Oligocene time.

On the basis of morphological similarity, and even intermediacy in some cases, the genus *Gopherus* is believed to have evolved from an early member of *Stylemys*, probably in western North America during the Late Eocene. The genus *Gopherus* is, and has always been, restricted to the Nearctic Realm. Its failure to migrate over Cenozoic land bridges to either Asia or South America was probably due to ecological factors.

The salient morphologic characters of the genus *Gopherus* are: a continuation of the palatal vomerine ridge upon the premaxillaries at their symphyses; short cervical vertebrae with an articular arrangement considered normal within the cryptodires; length of hypoplastron and hyoplastron about equal; forelimbs and claws flattened and widened; antebrachial scales juxtaposed, flattened, and broad; head scales small, flat, and rounded; eyes moderate in size; usually a single, large supra-caudal shield; alveolar surface of the upper jaw with an inner ridge running parallel with the cutting edge; alternate anterior neurals usually octagonal; anterior palatine foramina small; distal and proximal ends of humerus considerably expanded; tail very short; caudal vertebrae short and broad, without aberrant processes; skull wide, with a well developed post-orbital bridge, quadrate enclosing stapes; pro-otic exposed; shell broad, moderate in height; costal scutes low and broad; vertebral scutes wide; nuchal scute usually as wide, or wider, than long; hind foot short, elephantine, with short metatarsals; tibiale and fibulaire usually fused; carpus with a distinct proximal centrale, at least in the young, but often fused with an adjacent centrale in adults.

At the present time the genus is comprised of four allopatric populations that have long been considered distinct at the species level. The relegation of these populations to subspecific rank (Gray 1873; Mertens and Wermuth 1955) implies a degree of morphological similarity and an evolutionary history that is not consistent with our present knowledge. As will be shown below, the four Recent populations are morphologically distinct, although their superficial similarities often obscure important differentiating characters. Furthermore, fossil evidence based both on distinctness of form and at least partial overlap of geographic range during the same geologic period (Sangamon Pleistocene) suggests that the populations are distinct at the species level, and that they have been genetically separated from one another for a considerable length of time (Auffenberg, study in progress).

Hybrids resulting from a cross between captive *Gopherus agassizi* and *Gopherus berlandieri* have been described (Woodbury 1952; Mertens 1964), but the origin of at least one of the parents was uncertain

and its identification in doubt. More importantly, it is not known whether the young were infertile or not. Furthermore, hybridization between these two forms, even if proven, does not affect the relationship of either of them to *G. polyphemus* and/or *G. flavomarginatus*; inasmuch as *G. agassizi* and *G. berlandieri* are clearly more similar morphologically than either are to *G. polyphemus* or *G. flavomarginatus*. This view, held by several previous authors, is based on several morphological characters. Thus, *G. berlandieri* is more similar to *G. agassizi* than either is to *G. polyphemus* in alveolar angle, hind foot diameter, head width and proportionate shell height (True 1882; Bogert and Oliver 1945; Williams 1950a, 1952; Carr 1957; Legler 1959; Brattstrom 1961; Legler and Webb 1961; *et al.*). *Gopherus flavomarginatus* was considered more closely related to *G. polyphemus* than to either of the two remaining species by Legler (1959) and Legler and Webb (1961) on the basis of these characters and by Auffenberg (1966a) on the basis of carpal architecture. This conclusion is supported by the studies of Rose, Drotman, and Weaver (1969) on electrophoretic composition and separation of chin gland exudates. Grant's purely speculative statement (1960) that *flavomarginatus* may be a synonym of *agassizi* lacks supporting evidence.

The lack of knowledge concerning morphological variation in tortoise species is due largely to the difficulty of obtaining sufficiently large skeletal series. This is particularly true of fossil tortoises, where previous work usually has been based on the study of single specimens or very small samples. In this study large numbers of specimens of each of the four allopatric Recent populations were accumulated for osteological comparisons: *G. polyphemus*, 63 (Florida, Georgia, Alabama, and Louisiana); *G. agassizi*, 42 (Arizona, California, Utah, and Sonora); *G. berlandieri*, 54 (Texas, Tamaulipas, Coahuila and Nuevo Leon); and *G. flavomarginatus*, 24 (Durango).

The first and most important step in an investigation of this type is the selection of characters to be used. The concepts of size and shape are fundamental to such analyses. Shape tends to provide more reliable indications of relationships among reptiles than size (Jolicœur and Mosimann 1960; *et al.*). Careful study and comparison of the available Recent and fossil material indicate that certain structural details of the skeleton, scute proportions, and skeletal dimensions of the shell, limbs, and skull are probably the most useful and significant taxonomic characters. The exact nature of these and the method in which they were measured are identified and discussed below. These measurements are then analyzed.

Statistical treatment of linear measurements on reptiles is often complicated by the fact that objective criteria for identifying the growth

stage are lacking. In many studies on reptiles such difficulties are believed avoided by considering the relative size of single or multiple groups of unit characters. Most often this approach is essentially a univariate characterization, expressed as a ratio in which one variable is considered independent of the other. In many cases this independence is improperly assumed; in others it is difficult to establish. Statistically it is considered valid only if the variances of the two variables are similar (Kermock and Holdon 1950; *et al.*). To establish the best possible discrimination technique, a number of characters were analyzed by ratios, log-ratios, and actual measurements. The results of the comparative analysis clearly showed that log-ratio and simple ratio comparisons are less discriminatory than actual measurements in adults (see Tables 13-14). Three major types of statistical analyses based on actual measurements are employed in this paper: (1) univariate characterization, establishing the mean and standard deviation of all characters analyzed, (2) multivariate characterization of a number of differently combined sets of 36 variables on the shell, and (3) linear discrimination by means of the BIOMED 005 technique (Kendall 1951). Details of analyses will be found in specific sections below.

ACKNOWLEDGMENTS AND ABBREVIATIONS

Unless indicated otherwise all the specimens of extant populations upon which this study is based are in the collections of the Florida State Museum, University of Florida (UF). Fossil materials were examined from this same collection, plus that of the American Museum of Natural History (AMNH), Chicago Natural History Museum (CNHM), United States National Museum (USNM), University of Michigan, Museum of Zoology (UMMZ), Los Angeles County Museum (LACM), University of Arizona (UA), University of Texas (UTBEG), Academy of Natural Sciences of Philadelphia (ANSP), Panhandle Plains Historic Museum (PPHM), University of California, Museum of Paleontology (UCMP), Museum of Comparative Zoology (MCZ), University of Colorado Museum (UCM), University of Kansas, Museum of Natural History (UK), Charleston Museum (ChM), and Tulane University (TU). I wish to thank all of the persons in charge of these collections for allowing me to examine specimens in their care.

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OSTEOLOGICAL RESUME OF THE RECENT SPECIES

THE SKULL

Among testudinine turtles *Gopherus* has been recognized as possessing a distinctive skull, and it was on this basis that Gray (1873) established the Tribe Xenobatiana. It presents a complex of both primitive and specialized structures. The unique median premaxillary ridge is shared with the extinct genus *Stylemys*. In *Gopherus* the exposure of the pro-otic varies from completely visible to completely covered. An exposed pro-otic is generally considered a primitive condition (Loveridge and Williams 1957). An *Os transiliens* has been reported in all extant species (Ray 1959; Legler 1962; and Bramble 1974). The prefrontals are short (specialized), but still enter the orbit (generalized). The reduced postorbital in this genus is believed to be a specialization. The temporal region is broadly emarginate posteriorly. Although the jugal is small, the quadratojugal is well developed and frequently in contact with the maxillary. The quadrate is considered specialized because it encloses the stapes. The maxillary is specialized, and usually possesses three ridges: an outer cutting edge, one near the posterior edge of the expanded alveolar surface, and another between these. Although the anterior palatal foramina are large, they are somewhat concealed (primitive?), because the palate is highly vaulted (specialized). The basisphenoid is moderately small, and the ethmoid fissure moderately deep. The supraoccipital crest is short, and the orbits are placed well forward on the skull. A parietal foramen has been reported in *Gopherus polyphemus* (Zangerl 1957). In this study it was found in seven percent of *G. polyphemus*, and in five percent of *G. agassizi* specimens examined, but was never found in *G. berlandieri* or *G. flavomarginatus*. The lower jaw has lingual and lateral ridges, separated by the linear alveolar concavity. Both ridges are interrupted dorsal to the symphysis by a shallow antero-posterior groove. Eleven measurements (Fig. 1) were taken on the skulls of 133 specimens of *Gopherus* (6 *flavomarginatus*, 22 *agassizi*, 38 *berlandieri* and 67 *polyphemus*).

SEXUAL VARIATION.—There are no significant differences between the skull proportions of males and females in any of the Recent species of *Gopherus*; however, *G. berlandieri* males have proportionally larger heads than do females (Fig. 2).

ONTOGENETIC VARIATION.—The most obvious changes with growth are associated with the proportionate growth of the pre- and postorbital areas. The postorbital area exhibits considerably more growth than the preorbital area (Fig. 3). There is no significant interspecific difference

in allometric skull growth, although the skulls of *G. polyphemus* and *G. flavomarginatus* are considerably wider than those of *G. agassizi* and *G. berlandieri*.

INTRASPECIFIC POPULATION COMPARISONS.—Only in *G. polyphemus* is there sufficient material to make population comparisons. Two populations were compared, of which one comprised a sample of 44 specimens (from north-central Florida and the east coast of the Florida peninsula) and the other 23 specimens (from the Florida panhandle, southeastern Georgia, southern Alabama, and Mississippi). Specimens in the western sample have slightly wider heads than those in the eastern (peninsula) sample, a situation already suggested by Legler (1959) (greatest width of skull as percentage of condylobasilar length: western $\bar{X}=0.88$, eastern $\bar{X} 0.95$; $P=0.08$). The alveolar angle is wider in the eastern ($\bar{X} 82.5$) than in the western ($\bar{X} 67.5$) sample. When the series of *berlandieri* is separated into two samples (one north of the Rio Grande and another south of that river), the northern specimens seem to have a wider interorbital area, although the difference is not statistically significant ($P=0.42$). It is reasonable to assume that when more specimens are examined the character will be found to be geographically variable in *berlandieri*, perhaps even clinal.

INTERSPECIFIC DIFFERENCES.—It is shown in Table 1 that many structural skull features are shared by *G. polyphemus* and *G. flavomarginatus* on the one hand, and by *G. agassizi* and *G. berlandieri* on the other. The most obvious of these is the proportionate width of the skull, as measured at the widest point (across the postorbital bridge). *Gopherus polyphemus* and *G. flavomarginatus* have wide skulls, whereas *G. agassizi* and *G. berlandieri* have relatively narrow skulls. Mean proportional measurements (greatest skull width/condylobasilar length) of the four species are as follows: *polyphemus*, 0.88; *flavomarginatus*, 0.82; *agassizi*, 0.75; and *berlandieri*, 0.76. The difference between the means of *polyphemus* and *flavomarginatus* is not significant ($P=0.32$), as is also true in means of *agassizi* and *berlandieri* ($P=0.71$). When the data for both species in each group is grouped (*polyphemus*+*flavomarginatus* versus *agassizi*+*berlandieri*), however, the differences in combined means is highly significant ($P=0.01$). There is no significant difference in the interorbital width of these four species (Table 1).

Skull height is not significantly different in the four Recent species (Table 1), although Mexican specimens of *G. berlandieri* have proportionately higher skulls than those from Texas.

The postorbital bar shows considerable variation with regard to the shape of its constituent elements. To a certain extent, some variational

TABLE 1.—SKULL VARIATION IN *Gopherus* SPECIES.

Ratios and Measures	Species							
	<i>agassizi</i>		<i>berlandieri</i>		<i>flavomarginatus</i>		<i>polyphemus</i>	
	\bar{X}	OR	\bar{X}	OR	\bar{X}	OR	\bar{X}	OR
<u><i>l. prmx at symph.</i></u>								
condibasilar 1.	0.20	0.17–0.23	0.24	0.15–0.26	0.18	0.16–0.20	0.18	0.14–0.21
<u><i>gr. skull width</i></u>								
condibasilar 1.	0.75	0.65–0.88	0.76	0.67–0.83	0.82	0.77–0.86	0.88	0.77–0.97
<u><i>interorbital w.</i></u>								
condibasilar 1.	0.24	0.19–0.29	0.21	0.19–0.24	0.25	0.24–0.27	0.28	0.21–0.31
<u><i>skull height</i></u>								
condibasilar 1.	0.43	0.36–0.48	0.45	0.37–0.59	0.48	0.42–0.54	0.46	0.41–0.49
alveolar angle	72	69–79	74	66–81	77	74–80	79	76–84

patterns are species characteristic (Fig. 4). The same is true of the shape of the exoccipital bones and the position and size of their included foramina (Fig. 4).

The width of the alveolar surface of *G. polyphemus* and *G. flavomarginatus* is identical and is very wide when compared with that of the other two species. The alveolar surface of *berlandieri* is the narrowest of the four species, whereas *agassizi* is intermediate in this respect. Two alveolar ridges occasionally occur as an individual variant in specimens of all species. This somewhat primitive condition which seems most common in *flavomarginatus*, may be seen in an illustration by Gray (1873: pl. LX).

The outer alveolar angle of *G. polyphemus* and *G. flavomarginatus* is wider than that of *G. agassizi* and *G. berlandieri* (Table 1 and Figs. 5-8): *agassizi* has the least angle, with *berlandieri* intermediate between this species and *polyphemus-flavomarginatus*. The angle formed by the outer surface of the alveolar surface is directly related to the width of the skull. The above data are in agreement with those of other authors and confirm the idea that the differences in skull measurements are of a specific nature (Legler 1959; *et al.*).

Other more subjective characters are present that suggest the same general relationship (*polyphemus-flavomarginatus*, *agassizi-berlandieri*). These are (see also Figs. 5-8):

<i>polyphemus-flavomarginatus</i> group	<i>agassizi-berlandieri</i> group
1. Median longitudinal alveolar maxillary ridge always crosses premaxilla to contact median premaxillary ridge.	1. Longitudinal maxillary alveolar ridge frequently fails to cross premaxilla (especially in <i>berlandieri</i>).
2. Interpterygoid width greater.	2. Interpterygoid width less.
3. Basisphenoid shorter, anterior angle less acute (87-46°).	3. Basisphenoid usually longer, anterior angle usually more acute (52-28°).
4. Maxilla proportionately lower.	4. Maxilla usually proportionately higher.
5. When viewed through nasal opening: (a) dorsal projection of vomer longer.	5. When viewed through nasal opening: (a) dorsal projection of vomer generally shorter.

- | | |
|---|---|
| (b) anterior median groove on vomer shorter. | (b) anterior median vomer groove longer, running more anteriorly. |
| (c) palatine foramina usually smaller. | (c) palatine foramina usually larger (especially in <i>berlandieri</i>). |
| (d) dorsal, median foramen usually larger. | (d) dorsal, median foramen usually smaller (especially in <i>berlandieri</i>). |
| 6. When otic area is viewed from side (Fig. 9): | 6. When otic area is viewed from side (Fig. 9): |
| (a) lateroposterior wall of quadrate usually thinner. | (a) lateroposterior wall of quadrate usually thicker (especially in <i>berlandieri</i>). |
| (b) Stapes in groove to edge of tympanic excavation. | (b) Stapes not in groove to edge of tympanic excavation. |
| (c) Tympanic excavation with a rather smooth inner wall. | (c) Inner wall of tympanic excavation usually furrowed and ridged. |
| 7. Quadrate practically vertical when seen from side. | 7. Quadrate usually angled anteriorly (least in <i>berlandieri</i>). |
| 8. Pro-otic usually well exposed anteriorly (Table 2). | 8. Pro-otic usually not exposed anteriorly (Table 2). |
| 9. At symphysis of lower jaw: | 9. At symphysis of lower jaw: |
| (a) Median symphyseal length shorter. | (a) Median symphyseal length longer. |
| (b) Dorsal symphyseal groove (to receive median premaxillary ridge) narrower. | (b) Dorsal symphyseal groove usually much wider (especially in <i>berlandieri</i>). |

With regard to the basis of the skull and lower jaw, *G. agassizi* is intermediate in several important characters between *G. berlandieri* and *G. polyphemus-flavomarginatus*. *G. berlandieri* is the most specialized in many respects, although it is obviously closer to *G. agassizi* than to either of the remaining species.

TABLE 2.—CONDITION OF THE PRO-OTIC BONE IN *Gopherus* SPECIES.

	Exposed	Partly Concealed	Completely Concealed
<i>agassizi</i>	4	12	14
<i>berlandieri</i>	5	11	19
<i>flavomarginatus</i>	5	1	0
<i>polyphemus</i>	53	2	1

CERVICAL VERTEBRAE

In most living species of turtles the cervical vertebrae are quite variable in a number of respects. Often this variation is intraspecific in nature. It may include the number of vertebrae, length/width ratios, development of neural spines, transverse processes and ventral keels, number and degree of development of intervertebral ossicles, placement and shape of the zygapophyses, and in the number and placement of convexities and concavities forming the central joints. Of these, the last has been most extensively studied (Williams 1950b). Williams has clearly shown that the normal central-joint pattern (occipito-cervical joint excluded) is (2 (3 (4) 5) 6) 7 (8).¹ This is believed to be the primitive condition and was the only pattern he found in *G. agassizi* and *G. polyphemus*. Of 19 specimens of *berlandieri*, however, six had the pattern (2 (3) 4) 5) 6) 7 (8) and three had the pattern (2 (3) 4) 5) 6) 7) 8). Both variations are specializations tending toward procoely. Additional data obtained during the course of this study substantiate the major features of the intraspecific differences in this genus suggested by Williams (Table 3). It is significant that divergence from the normal pattern occurs only in *agassizi* and *berlandieri* and is of a similar type. There is no divergence from the normal pattern in *polyphemus* and *flavomarginatus*.

TABLE 3.—CERVICAL JOINT PATTERN VARIATION (IN %) WITHIN *Gopherus* SPECIES.

Species	Normal	Patterns	
		4th joint variation	7th joint variation
<i>agassizi</i>	77.7	16.7	5.6
<i>berlandieri</i>	51.0	32.3	16.7
<i>flavomarginatus</i>	83.3	16.7	0.0
<i>polyphemus</i>	94.4	5.6	0.0

CAUDAL VERTEBRAE

The number of caudal elements in *Gopherus* vary from 12 to 19. The first five to six elements are often incompletely ossified, so that the

¹ (= convexity anteriorly;) = convexity posteriorly; and () = convexity both anteriorly and posteriorly.

neural arch pedicles are not fused to the centra. The first three centra are platycoelous; the rest are procoelous. At the anterior end of the series the vertebrae are somewhat elongated and as high as wide. Posteriorly they become noticeably flattened and much wider than long. The last two or three centra are often fused and may lack transverse processes. Pre- and postzygapophyses are well developed throughout the series, with the exception of the last few fused members. The transverse processes are rarely firmly ankylosed to the pedicle-centrum suture area. In the most posterior 10 to 11 elements the transverse process is also in contact with the posterolateral corner of the preceding centrum. Adjacent transverse processes are often fused near the posterior end of the series. An interpostzygapophyseal notch is always present. The transverse processes are normal in length from the anterior part of the series to near the point of the base of the external tail. Here the processes are most elongated, decreasing rapidly in length to the terminus of the tail. If the terminal tips of the transverse processes are considered as an outline of the bony skeleton of the tail, the overall shape is broadly spatulate. Subcaudal dermal ossicles are often fused to the underside of the last 8 to 10 vertebrae. Differences observed in the caudal series of *Gopherus* (Recent and Pleistocene only) and the closely related genus *Stylemys* are as follows:

<i>Gopherus</i>	<i>Stylemys</i>
Interpostzygapophyseal notches present throughout series.	Interpostzygapophyseal notches usually absent from most vertebrae, and always absent from some of the middle members of the series.
Neural spine, boss, or keel absent from all caudal vertebrae.	Neural spine, boss, or keel absent from only the anterior caudal vertebrae.
Post- and prezygapophyseal articular surfaces normal, separated, distinct.	Post- and prezygapophyseal articular surfaces transversely elongate, often continuous.

Unfortunately, the tail tip in *Stylemys* remains unknown. I have found no significant interspecific differences among the extant populations of the genus *Gopherus*.

HUMERUS

The humerus of *Gopherus* is like that of most other testudinid turtles. Proximal condyle round, rarely slightly compressed vertically; shaft slightly compressed, noticeably bent in the middle. Distal end compressed anterolaterally, broadly widened laterally. Medial proximal tu-

berosity larger than in most testudinines; not greatly projecting medially and higher than lateral process. Lateral process directed lateroposteriorly, with the angle between it and the medial tuberosity small. Posterior intertubercular excavation completely open and well developed. No humeral depression for attachment of the deltoid muscle, which inserts on a low ridge below and slightly lateral to the condyle. Entepicondylar foramen slit-like, sometimes obliterated. Radial and ulnar condyles well developed, but not clearly differentiated from each other.

The extant species do not differ greatly in humeral proportions (Table 4), although the humeral shaft is slightly thicker in *G. flavomarginatus* than in the remaining species, and the distal expansion is proportionately narrower. The distal width of the humerus is identical in *G. agassizi* and *G. berlandieri*, although *agassizi* has a slightly wider proximal width.

TABLE 4.—HUMERAL PROPORTIONS IN *Gopherus* SPECIES.

<i>Greatest Proximal Width/Least Shaft Width:</i>				
<i>agassizi</i>	OR 2.4–3.5	\bar{X} 3.0	SD \pm 0.22;	N 20
<i>berlandieri</i>	OR 2.4–3.5	\bar{X} 2.9	SD \pm 0.32;	N 35
<i>flavomarginatus</i>	OR 2.5–3.0	\bar{X} 2.7	SD \pm 0.43;	N 13
<i>polyphemus</i>	OR 2.6–3.8	\bar{X} 3.1	SD \pm 0.24;	N 28
<i>Greatest Distal Width/Least Shaft Width:</i>				
<i>agassizi</i>	OR 2.5–3.8	\bar{X} 3.1	SD 0.31;	N 20
<i>berlandieri</i>	OR 2.3–3.8	\bar{X} 3.1	SD 0.33;	N 35
<i>flavomarginatus</i>	OR 2.6–3.3	\bar{X} 2.9	SD 0.36;	N 13
<i>polyphemus</i>	OR 2.8–3.8	\bar{X} 3.3	SD 0.28;	N 28
<i>Greatest Proximal Width/Greatest Distal Width:</i>				
<i>agassizi</i>	OR 0.80–1.05	\bar{X} 0.98	SD 0.42;	N 20
<i>berlandieri</i>	OR 0.80–1.02	\bar{X} 0.93	SD 0.38;	N 35
<i>flavomarginatus</i>	OR 0.78–1.01	\bar{X} 0.91	SD 0.32;	N 13
<i>polyphemus</i>	OR 0.86–1.21	\bar{X} 0.98	SD 0.61;	N 28

PELVIC GIRDLE

The species of living *Gopherus* differ little in respect to their pelvic girdle proportions. In all of them the obturator foramen is large, and usually more oval in *G. polyphemus* and *G. flavomarginatus* than in the other two species. The epipubic area is well developed anteriorly, being widest in *polyphemus*, narrowest in *agassizi* and *berlandieri*, and intermediate in *flavomarginatus* (Figs. 10–13). The pubic process is not as well developed as in most turtles, and typically is variable in its length and orientation. In all species, except *flavomarginatus*, it is located approximately halfway between the acetabulum and the anteromedial corner of the pubis. In *flavomarginatus* the process is located much

closer to the epipubic process. The remainder of the girdle is similar in all four recent species.

FEMUR

The femur of testudinid turtles is distinguished from that of emydid turtles by a ridge that runs nearly on the level of the proximal condyle and connects the medial and lateral trochanters. Between this ridge and the condyle there is a pit, the *fossa intertrochanterica*. The proximal condyle is set at an oblique angle, is oval in outline, and is more compressed in *G. agassizi* and *G. berlandieri* than in the two remaining species (Figs. 10-13). The shaft is slightly curved and not compressed. It is proportionately widest in *flavomarginatus*. The distal end is greatly expanded laterally and compressed anteroposteriorly. In adults the distal condyles are well developed, separated by an intertubercular sulcus. They are most clearly differentiated in *flavomarginatus* and *polyphemus* and weakly developed in *agassizi* and *berlandieri*.

CARPUS

Primitively the turtle carpus contained 10 elements (radius, intermedium, ulnare, centrale, pisiform, and five carpals). Apparently the centrale was not in contact with either the radius or the ulna. In presumably primitive tortoises, such as *Geochelone denticulata*, the carpus is composed of 10 elements, at least in the embryonic stage (Hoffman 1890). In this species the centrale has moved distally, so that it contacts the radius; the pisiform is small and in contact with the ulna and carpal 5, instead of only the latter. This pattern is apparently basic in land tortoises. Its modifications include fusion or loss of elements, both of which are individually and ontogenetically variable.

In cleared and stained forelimbs of very young *Gopherus*, I have never found more than nine carpal elements. The pisiform is apparently lost. Furthermore, there is considerably more fusion of the elements in adult *Gopherus* than in any other genus I have studied (Auffenberg 1966a). This is probably associated with the use of front limbs for excavating burrows and shelters.

An examination of many articulated feet of the species of this genus suggests that, although there is considerable variation in the degree of fusion of the component distal elements, two basic patterns are discernible (Auffenberg 1966a). One is found in the *G. polyphemus-flavomarginatus* group, where six carpal elements are in contact with the ulna and radius. In the *G. berlandieri-agassizi* group only four or five elements are in contact with the two brachial elements.

The carpus of *Gopherus* has been shown to represent a primitive type among tortoises (Auffenberg 1966a). It is distinguished by two features:

a separate proximal centrale, at least in the juveniles; and the position and shape of carpal 4, which completely separated the ulnare from medial 3.

Carpi were examined in 32 specimens of *G. polyphemus*, 7 of *G. flavomarginatus*, 31 of *G. agassizi*, and 37 of *G. berlandieri* with the following results:

Gopherus polyphemus—Except for a slight difference in degree of phalangeal fusion in digit 5, there is little variation correlated with tortoise size. The proximal centrale is present in all specimens. Carpal 1 is fairly large and articulates broadly with the radius, the radius being bordered below by four elements (carpal 1, radiale+mediale 2, proximal centrale, and intermedium). There are no intercarpal fusions and the metacarpals are typically fused to adjacent phalanges (14 of 32 specimens in all 5 digits, 18 in all digits except number 5). Carpal 4 is wedged between the ulnare and mediale 3, but not so extensively as in *G. agassizi* and *G. berlandieri*. Carpal 5, the ulnare, and intermedium are all in broad contact with the ulna. The pisiform is absent in all but three specimens.

Gopherus flavomarginatus—The carpus in this species is similar to that of *G. polyphemus*, with four subradial elements (carpal 1, radiale+mediale 2, proximal centrale, and intermedium), and three subulnar elements (intermedium, ulnare and carpal 5). The metacarpals are fused to adjacent phalanges.

Gopherus agassizi—The arrangements of elements in *G. agassizi* is different from those of *G. polyphemus* and *G. flavomarginatus* and similar to that of *G. berlandieri*. The proximal centrale sometimes is a separate element, as in *G. polyphemus*; this was observed in four of eight specimens smaller than 150 mm shell length and in 11 of 23 larger specimens. In those smaller specimens lacking a separate proximal centrale, the bone is fused to the intermedium. In all 11 larger specimens having a separate proximal centrale, carpal 1 is fused to the composite radiale, whereas in 10 of the other 12 specimens (*i.e.* in which the proximal centrale was fused to the intermedium), carpal 1 is free in 21 of the 23 specimens over 150 mm, although in some the fusion is not complete. No such fusion can be seen in six of eight specimens less than 150 mm in shell length. The radiale and mediale 2 and 3 are solidly fused together in 11 specimens over 150 mm, and in all individuals carpals 1 and 2 are also fused into this mass. Carpals 1 and 2 are fused in 21 of the specimens over 150 mm. All the metacarpals are fused to the adjacent phalanges in all specimens examined, regardless of size. Carpal 5 is fused to both the pisiform and ulnare in 13 of the 23 specimens over 150 mm; in every larger individual in which carpal 5 is free, the pisiform is fused

to the ulnare. The pisiform is free in all the smaller specimens examined.

These data show that the carpus of *G. agassizi* is more variable than that of *G. polyphemus*, particularly in the lateral elements of the subradial and subulnar complexes.

Gopherus berlandieri—The lack of a separate proximal centrale, plus several other anatomical features, suggest that *G. berlandieri* is closer to *G. agassizi* than to the other two extant species. In six specimens under 100 mm in shell length, mediale 2 is not fused to the composite radiale, as it is in all specimens over 100 mm in shell length. In no specimen is the proximal centrale separate from the intermedium. Carpal 1 is separate and in contact with the radius in all specimens and is never fused to the composite radiale. Metacarpals 3 and 4 are always fused to the adjacent phalanges, but metacarpals 1, 2, and 5 are fused to the adjacent phalanges in only the larger specimens. The pisiform is always present. Carpal 5 is fused to the ulnare in 22 of 41 individuals over 100 mm, and carpal 4 separates mediale 3 and the ulnare in all specimens. The radiale is fused to mediale 2 in all individuals, and these are fused to mediale 3 in all adult specimens.

The major difference between the carpus of the *polyphemus* and *berlandieri* groups seems to lie in the position of the centrale. In the former it is in its primitive tortoise position, *i.e.* in contact with the radius. In the *berlandieri* group it is excluded from contact with the radius by the intermedium (Fig. 14). In the *polyphemus* group loss and fusion of carpals and metacarpals occur along the axis of digits II, III, IV and V. When fusion occurs in the *berlandieri* group, it does so along the axis of digits I, IV and V (Table 5).

TARSUS

The tarsus of tortoises is evidently more conservative than the carpus. In *Gopherus* I found no significant interspecific differences in the tarsus. The tibiale, intermedium, and centrale are always completely fused in adults, and the fibulaire is usually separate. In most other tortoises this element is also fused to the large composite element. The tarsals are either four or five in number; if the former, then tarsals 4 and 5 are fused, rather than 3 and 4 as in most turtles (Hoffman 1890). All five metatarsals are distinct, with number 1 being the most robust, as is generally true in all turtles. Metatarsals IV and V articulate with separate tarsals, or with only one if tarsals 4 and 5 are fused. Two phalanges are always found on digits I through IV. The phalanges of digit V are often missing, although one is sometimes present (Fig. 14).

DERMAL ARMOR

Dermal ossicles in *Gopherus* are mainly developed in three areas:

TABLE 5.—CARPAL AND METACARPAL FUSION AND/OR LOSS PATTERNS IN *Gopherus*.

	<i>berlandieri-agassizi</i>	<i>polyphemus-flavomarginatus</i>
axis of digit I	usually all present, but C ¹ frequently fuses with M ¹	all present
axis of digit II	all present, though C ² may fuse to M ¹ and C ³ , never to the radiale	all present, though the radiale may be fused to C and C ³ in adults.
axis of digit III	Centrale and intermedium always fused. C ³ may be fused to C ² . (C ³ may be fused to radiale and intermedium in adults)	C ³ in contact with centrale and the intermedium (fused to these and the radiale in large adults).
axis of digit IV	C ⁴ missing (if ulnare fused, then to C ⁵)	C ⁴ missing (ulnare fused to intermedium in adults)
axis of digit V	C ⁵ present in young, fused to ulnare in adults	C ⁵ missing in young and adults

the posterior surface of the thighs, the hind foot, and the forearm. These ossicles, which are covered by horny scales, vary ontogenetically, sexually, individually, interspecifically, and geographically; the most obvious variation is interspecific. The anterior forelimb ossicles of both *G. polyphemus* and *G. flavomarginatus* are usually flattened, and though variable in shape, are usually hexagonal or pentagonal (Fig. 16). Those of adult *flavomarginatus* are often very thick and sometimes partially fused. A single scale on the anteromedial surface opposite the elbow is noticeably enlarged, particularly in *polyphemus* and *flavomarginatus*. This scale may be important in courtship (Auffenberg 1966b). The scales at the outer edge of the forearm are usually longer and more spine-like in all the species. In *G. agassizi* and *G. berlandieri* the ossicles of the anterior surface of the forearm are more imbricate and are often keeled and spine-like. *G. agassizi* is much more variable than *G. berlandieri* in this character, and the variation may be geographically correlated. The material available is insufficient to prove this, however.

The dermal ossicles of the thigh are usually best developed in large males. They are often arranged in a circular patch, with one or two central members largest. They are best developed in *G. flavomarginatus*, where they are cone-like in adults. In *G. polyphemus* they are often completely flattened.

The dermal ossicles of the hind foot are best developed on the posterior surface of the foot at the heel. Males tend to have larger heel spurs than females. They are best developed in *G. flavomarginatus*.

RADIUS AND ULNA

The radius is always the larger of the two elements. Its curvature and proportions are slightly different in *G. polyphemus* and *G. agassizi*, although there is considerable overlap and single elements of the two species usually cannot be separated. In general, the radii in both *berlandieri* and *polyphemus* are flatter and less curved than that of *agassizi* (Figs. 10-13). *G. flavomarginatus* has a radius similar to that of *polyphemus*. In large adults it is often possible to discern the number of carpal elements that had articulated with the distal end of the radius. Four facets are usually evident in *polyphemus* and *flavomarginatus*, and two or three in *berlandieri* and *agassizi*. This is of particular importance in the study of fossil radii.

The ulna in all land tortoise genera is considerably shorter than the radius. The ulna is very similar in all the extant species but occasionally is more twisted in *berlandieri* and *agassizi* than in *polyphemus* and *flavomarginatus*.

SHELL

At hatching the young gopher tortoise possesses only the most rudimentary elements of the bony shell (Fig. 18). These are the vertebrae, the ribs (which extend to the edge of the costal scutes), and the small centers of ossification at the posterior lower corner of each of the anterior and posterior marginal scutes. The plastral buttresses are long and provide maximum support until the shell is completely ossified. The axillary buttress extends to near the junction of the lateral anterior corner of vertebral scute 1 and costal scute 1. The posterior inguinal buttress lies just anterior to the sixth rib, and extends approximately one-fourth of the way medially. Later in development the ends of the buttresses come to be located closer to the distal rib ends (Fig. 18). All of the plastral bones, except for the entoplastron, are more heavily ossified than those of the carapace. The epiplastral lip is not greatly projected, and there is no deep excavation behind.

With increasing age and progressive ossification of the shell, the shallow grooves on the dorsal edge of the peripherals (in which distal ends of the rib were originally located) become modified to shallow pits (Fig. 18). In addition, there are important changes in the hypoplastral-xiphiplastral articulation.

In general, ontogenetic change in shell shape (viewed from above) is from a more rounded to a more elongate outline. This is much more evident in *polyphemus* than in *berlandieri* or *agassizi* (Fig. 19). I have not seen any hatchlings of *flavomarginatus*.

The general shell characteristics of Late Tertiary, Pleistocene, and Recent adult specimens of *Gopherus* are: shell of moderate height, with moderate anterior and posterior openings; plastron extending beyond anterior margin of carapace; anterior edge of carapace transverse to concave; marginals with entire edges, not deeply serrated but often with small pointed projections at scute sulci; no hinge in either carapace or plastron; width of vertebral scutes greater than length and about equal to height of costal scutes, which in turn are about equal to bridge marginals; last vertebral scute almost always as wide as caudal scute and two last marginals; bridge moderately long, without a well developed continuous keel; bones of shell thin; usually two suprapygals, the anterior one either A-shaped and embracing the posterior one, or placed on top of the other; one supracaudal scute, which is wider than the pygal bone; 11 marginal scutes; 11 peripheral bones; pleurals alternately wider and narrower medially and laterally; neural formula usually 4-8-4-8-4-(6-(6-(6, with the vertebral sulci usually crossing neurals 1, 3, 5 and 8; nuchal scute usually as wide or wider than long; rib heads slender, but relatively

short; epiplastral lip projecting, frequently with notches anteriorly and deeply excavated behind; inguinal and axillary scales present; inguinal buttress contacting underside of pleural 6 near distal end of rib (in adults); hyoplastral median length divided by hypoplastral median length, almost always 1.0 or more (Table 6).

TABLE 6.—HYO-HYPOPLASTRAL RATIOS IN *Gopherus* SPECIES.

Species	Hyo-Hypoplastral	
<i>agassizi</i>	$\bar{X} = 1.24$	$SD = \pm 0.07$
<i>berlandieri</i>	$\bar{X} = 1.24$	$SD = \pm 0.03$
<i>flavomarginatus</i>	$\bar{X} = 1.36$	$SD = \pm 0.58$
<i>polyphemus</i>	$\bar{X} = 1.16$	$SD = \pm 0.02$

Adult specimens show many sexual differences in the shell, most of which will be discussed below. The most noticeable is the shape of the plastral surface. In adult males there is a fairly large, slightly concave area centered near the xiphi-hypoplastral suture (least developed in *polyphemus*, best developed in *berlandieri*). When it occurs, this difference can usually be detected in specimens with a shell length of 150 mm or more. In females and young the plastron is flat.

SCUTE AND BONE ABNORMALITIES.—Sufficient skeletal material of the Recent species of *Gopherus* is available to establish the occurrence of at least the more common abnormalities of the shell. These are much more common than generally presumed, only 25 percent of all Recent *Gopherus* examined being free of any abnormalities.

Fourteen different anomalies are noted, seven in the scutes and seven in the bony plates (Fig. 20). Abnormalities in the bony plates are far more common than in the scutes. Scute abnormalities of several types occur in six different scutes: abdominal (partial and complete division), nuchal (deletion or addition of scutes), supracaudal (vertically divided), gular (divided, or failing to reach the entoplastron), vertebral (divided transversely or diagonally), and costal (additional scute, or divided transversely).

Abnormalities in the bony plates include various additions or deletions in the area of the last few neurals, the first supracaudal, second supracaudal; and additional elements at the proximal end of any of the last few pleurals, the first pair of pleurals, or the first neural (Fig. 20). Anomalies in the area of the first and second suprapygals are most common (Table 7), accounting for 57 percent of all the anomalous specimens.

The Recent species of *Gopherus* differ from one another with regard to percentage of abnormal specimens recorded and types of abnormali-

TABLE 7.—SHELL ABNORMALITIES IN *Gopherus* SPECIES.

Abnormalities	<i>agassizi</i>	<i>berlandieri</i>	<i>flavomarginatus</i>	<i>polyphemus</i>	Totals
BONES					
3 suprapygals	6	1	0	1	8
Suprapygals 1 not embracing 2	20	6	0	10	36
Suprapygals 1 + 2 fused	1	0	0	0	1
Divided suprapygals 2	0	1	0	0	1
Divided last neural	0	1	0	1	2
Divided first neural	2	0	0	1	3
Divided pleurals	1	0	0	0	1
SCUTES					
No nuchal	0	3	0	0	3
Extra nuchals	0	0	2	0	2
Extra or fused marginals	11	6	1	4	22
Divided supracaudal	0	2	0	0	2
Extra abdominals	2	0	0	0	2
Divided vertebrals	1	0	0	0	1
gulo-pectoral sulcus fails to enter entoplastron	11	4	0	1	15
Extra or fused costals	4	1	0	0	5
Total Normal	4	11	1	13	
Total Abnormal	31	24	3	25	

ties found. At least one abnormality occurs in either the scutes or bones of the following percentages of specimens examined: *G. polyphemus* 52%; *G. agassizi* 80%; *berlandieri* 72%; and *flavomarginatus* 66% (Table 8). The different abnormalities are not completely independent of one another; for example, in *G. agassizi* there is a significant correlation between the failure of the gular scute to overlap the entoplastron and the presence of one of the other abnormalities (chi square = 0.02).

NON-SPECIES CORRELATED QUALITATIVE VARIATION.—The neural formula (the sequence of quadrangular, hexagonal, or octagonal members in the neural series) is one of the most characteristic features of the family Testudinidae. Especially important is the fact that the series contains octagonal members that alternate with quadrangular members. The formula shows greater variation in *Gopherus* than in other genera of the family studied so far, and this variation is both bilateral and serial.

The most important of the serial variations is that existing between the anterior and posterior members of the series. Of these two areas, only the anterior is characteristically composed of elements that are al-

ternately quadrangular and octagonal. The posterior members are normally 4- or 6-sided; if the latter, the broad end of the hexagon faces anteriorly. All the neurals are generally hexagonal, with the broad end facing anteriorly in the emydid turtles. This arrangement is thought to represent the ancestral condition.

TABLE 8.—CORRELATED SHELL ABNORMALITIES IN *Gopherus* SPECIES.

	Neural or Vertebral	Pleural or Costal	Epiplastral or Gular	Plastral or Abdominal
<i>agassizi</i>				
Neural or Vertebral	2	1	7	1
Pleural or Costal	—	0	1	0
Epiplastral or Gular	—	—	0	1
Plastral or Abdominal	—	—	—	0
<i>berlandieri</i>				
Neural or Vertebral	3	0	2	0
Pleural or Costal	—	0	0	0
Epiplastral or Gular	—	—	0	0
Plastral or Abdominal	—	—	—	0
<i>polyphemus</i>				
Neural or Vertebral	2	0	0	0
Pleural or Costal	—	0	0	0
Epiplastral or Gular	—	—	0	0
Plastral or Abdominal	—	—	—	0

During the early phases of carapaceal ossification a single pair of ribbon-like pleurals is associated with each of the still undifferentiated, plate-like neurals. After this developmental stage is reached, the growth pattern of the proximal end of the pleural is exceedingly important in the final configuration of the neural (Fig. 21). Thus, in emydids and primitive testudinids the growth pattern of the proximal end of the pleural is such that posteriorly it grows more rapidly than it does dorso-anteriorly. This produces the neural formula 4-(6-(6-(6-(6-(6-(6, with the broad ends of the hexagons directed anteriorly (direction shown by "(") (Fig. 21). If the growth pattern of the proximal pleural end is such that the anterior edge grows faster than the posterior edge, the neural formula eventually produced is 4-6)6)6)6)6); if lateral growth in both directions is equal, the neural formula will be 4-8-4-8-4-8-4 (the typical, more specialized tortoise pattern); if every other pleural grows more posteriorly than anteriorly, the formula will be 4-6)4-6)4-6)4; and if every other pleural grows more anteriorly than posteriorly, the formula will be 4-(6-4(6-4(6-4. All these patterns can be found in *Gopherus*, often in serial or bilateral combination in one specimen. There is a

TABLE 9.—VARIATION IN THE SHAPE OF THE FIRST FIVE NEURALS IN THREE SPECIES OF *Gopherus*.¹

<i>berlandieri</i>	<i>agassizi</i>	<i>polyphemus</i>
(D) 4-8-4-8-4 (70%)	(D) 4-8-4-8-4 (50%)	(D) 4-8-4-8-4 (47%)
(½D) 4-7-4-7-5 (5%)	(½D+D) 4-7-5-8-4 (3½%)	(D+½E) 4-8-4-8-5 (8%)
(D+E) 4-8-4-8(6 (10%)	(D+C) 4-8-4-6(6) (3½%)	(D+½B) 4-8-5-5-4 (8%)
(D+E) 4-8-4(6-4 (5%)	(D+½D) 4-8-5-7-4 (3½%)	(½D) 5-7-4-7-4 (8%)
(B+½D+D)(6-7-4-8-4 (5%)	(D+½C) 4-8-5-5-4 (3½%)	(D+E) 4-8-4-8(6 (13%)
(½B+B+D) 4-5(6-8-4 (5%)	(D+C+½C) 4-8-6-5-5 (3½%)	(D+F) 4-8-6-4-6 (8%)
	(D+F+½E) 4-8-6-4-5 (3½%)	(D+A+F) 4-8-4-4-6 (8%)
	(B+D) 4(6(6-4-8 (3½%)	
	(C+D) 6(6)6)8-4 (3½%)	
	(C+½C+E) 6)5-6(6)4 (3½%)	
	(D+E) 4-8-4(6-4 (7%)	
	(½C+C+½C+C) 5-6(6)5-6 (3½%)	
	(B+½B) 4(6(6-5(6 (3½%)	
	(B+F) 4(6(6-4(6 (3½%)	

¹A = each pleural grows laterally at same rate (4-4-4-4-4); B = each pleural grows anteriorly (4(6(6(6(6); C = each pleural grows posteriorly (4(6(6(6(6); D = alternate pleurals grow laterally at same rate (4-8-4-8-4); E = alternate pleurals grow anteriorly (4(6-4(6-4); F = alternate pleurals grow posteriorly (4-6(4-6(4); 1/2 = suture characteristic on one side only. For additional explanation see text.

definite tendency for the anterior neurals to show greater differentiation than the posterior members, and thus the familial neural characteristics of the Testudinidae are usually restricted to the first few neurals. However, in *Gopherus* even the anterior neurals show considerable variation in growth pattern (Table 9), although some conceivable combinations of growth patterns have not yet been found. There is no significant difference between the neural growth patterns exhibited in the four species of *Gopherus* (Table 10). It can be seen in Figure 22 that the pleural growth pattern (in which there is alternate equal growth of the proximal ends of the pleurals) is the most common type when each neural is taken as an independently developed unit.

TABLE 10.—PLEURAL GROWTH PATTERNS IN SPECIES OF *Gopherus* INFERRED FROM NEURAL PATTERNS.

Species	Pleural Growth Patterns					
	A	B	C	D	E	F
<i>agassizi</i>	0	3	6	22	2	2
<i>berlandieri</i>	0	2	0	28	3	0
<i>flavomarginatus</i>	0	0	0	3	1	0
<i>polyphemus</i>	1	0	0	15	3	1

It has been said that in all New World tortoises, including *Gopherus*, the usual suprapygial condition is one in which the first suprapygial embraces the second. My findings do not entirely agree, since this condition was not found in about 39% (71) of the 183 *Gopherus* specimens I examined (*polyphemus* 28 [44%], *agassizi* 26 [62%], *berlandieri* 15 [28%], *flavomarginatus* 2 [8%]). It is clear that in *Gopherus* this variation is the direct result of a rather simple developmental phenomenon. In specimens with a carapace length of about 150 mm, in which the suprapygals are not yet fully ossified, there is a fenestrum on either side of suprapygial 2. These fenestrae eventually become filled with bone originating from only one of two centers of ossification (*i.e.* either one or the other of the two suprapygals). Should the ventro-lateral corners of the first suprapygial grow downward to fill the fenestrae, an embrasure will be formed. However, if during ossification the fenestrae are filled from the second, lower center of ossification, the first suprapygial will not embrace the second (Fig. 23).

All emydids and some of the testudinids (*Testudo*, etc.) possess the non-embracing type of pattern (Loveridge and Williams 1957). The earliest known fossil testudinids (*Geochelone* [subgenus *Hadrianus*] and *Stylomys*) possess the embrasure. So do almost all the available Tertiary specimens of *Gopherus*. Thus, the lack of an embrasure in Recent *Gopherus* is presumed to be secondary, and due to a simple change in

the pattern of ossification. This pattern is coincidentally identical to the more primitive, pre-testudinine pattern because only two major types are possible. Fenestral ossification is usually bilaterally correlated, so that if one center of ossification fills the fenestra on one side, the same center tends to do so on the other side as well. In some specimens the right and left sides do not develop identically (Fig. 24).

QUANTITATIVE SHELL VARIABLES.—The purpose of this portion of the study was to determine those combinations of characters that would best separate the adult specimens of the four species of *Gopherus*, and to establish how widely they are separated. The sample analyzed consisted of 183 adult *Gopherus*, including an approximately equal number of males and females of each species. From each of the shells available for study 49 measurements were obtained, 25 on the plastron (Fig. 25) and 24 on the carapace (Fig. 26). To simplify computation and comparison, these two parts of the shell were analyzed independently. Other variables considered early in the study were sex and population (= species). Accumulated data are provided in Table 11.

Relative variability of the characters investigated was first established by analysis of the coefficients of variation ($=\overline{CV}$) exhibited by the measurements. These are summarized as follows:

PLASTRON

- 1) Different parts of the plastron are differentially variable (Range \overline{CV} = 11.13 to 57.54; \overline{CV} = 21.31).
- 2) In different species the same characters do not vary in the same direction, or to the same degree.
- 3) Variation of scute length along median line (\overline{CV} = 22.68) does not differ significantly from variation in bone length along median line (\overline{CV} = 23.80) (Fig. 27).
- 4) Plastral variation in males is not significantly different from that of females (males \overline{CV} = 21.19, females \overline{CV} = 22.45) (Table 12). Within the species *polyphemus*, females are significantly more variable than males (males \overline{CV} = 18.52, females \overline{CV} = 26.80), but sexual variation is not significantly different in the three remaining species (*agassizi* males \overline{CV} = 22.60, females \overline{CV} = 22.70; *flavomarginatus* males \overline{CV} = 23.15, females \overline{CV} = 24.05; *berlandieri* males \overline{CV} = 21.81, females \overline{CV} = 18.79).
- 5) None of the species differ significantly from one another in total plastral variability (\overline{CV} for all plastral measurements in *polyphemus* = 22.76, *flavomarginatus* = 25.06, *agassizi* = 23.79, *berlandieri* = 26.26) (Table 12).

CARAPACE

- 1) Different parts of the carapace are differentially variable (Range \overline{CV} = 2.00-162.94, \overline{CV} = 29.80).
- 2) Variation in different parts of the carapace are species-dependent.
- 3) Variation of carapace scutes (\overline{CV} = 38.36) is not significantly different from variation of carapace bones (\overline{CV} = 30.87) (Table 12).
- 4) Males (\overline{CV} = 29.01) are significantly less variable than females (\overline{CV} = 36.63) when all species are combined. There is no significant difference in the mean variance of males (\overline{CV} = 29.80) and females (\overline{CV} = 32.27) in *berlandieri*. How-

TABLE 11.—SHELL STATISTICS, *Gopherus agassizi*.

Measure- ments ¹	Males (N=11)		Females (N=13)		Combined (N=24)	
	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV
PL	191.20 \pm 39.36	20.59	175.76 \pm 32.46	18.47	181.48 \pm 35.24	19.42
G	31.20 \pm 8.31	26.63	25.59 \pm 5.33	20.83	27.67 \pm 7.00	25.30
H	50.90 \pm 10.16	19.96	42.82 \pm 9.28	21.67	45.81 \pm 10.22	22.31
P	15.20 \pm 3.65	24.01	14.47 \pm 4.35	30.06	14.74 \pm 4.04	27.41
AB	58.10 \pm 10.01	17.23	56.18 \pm 10.40	18.51	56.89 \pm 10.10	17.75
F	27.00 \pm 5.98	22.15	25.35 \pm 5.17	20.39	25.96 \pm 5.43	20.92
A	17.80 \pm 3.52	19.78	17.88 \pm 3.97	22.20	17.85 \pm 3.74	20.95
ND	12.20 \pm 4.32	35.41	8.06 \pm 2.51	31.14	9.59 \pm 3.81	39.73
NW	22.70 \pm 5.52	24.32	17.82 \pm 6.50	36.48	19.63 \pm 6.51	33.16
XH	9.60 \pm 1.96	20.42	9.06 \pm 2.33	25.72	9.26 \pm 2.18	23.54
XL	41.50 \pm 6.82	16.43	38.06 \pm 6.92	18.18	39.33 \pm 6.96	17.70
XW	46.80 \pm 9.59	20.49	44.41 \pm 8.47	19.07	45.30 \pm 4.15	19.43
POL	56.10 \pm 12.91	23.01	50.24 \pm 10.40	20.70	52.41 \pm 11.51	21.96
HYP	38.60 \pm 6.60	17.10	38.94 \pm 7.03	18.05	38.81 \pm 6.75	17.39
HYO	48.00 \pm 9.94	20.71	43.53 \pm 8.65	19.87	45.19 \pm 9.23	20.43
EL	40.00 \pm 7.72	19.30	36.94 \pm 7.77	21.03	38.07 \pm 7.75	20.36
EW	38.80 \pm 9.76	25.16	35.82 \pm 8.41	23.48	36.93 \pm 8.87	24.02
ME	28.30 \pm 10.12	35.76	20.24 \pm 4.22	20.85	23.22 \pm 7.89	33.97
GE	48.70 \pm 13.39	27.50	38.82 \pm 8.74	22.51	42.48 \pm 11.52	27.12
AL	72.90 \pm 18.46	25.32	58.29 \pm 11.20	19.21	63.70 \pm 15.71	24.66
LT	13.10 \pm 2.13	16.25	11.71 \pm 2.54	21.69	12.22 \pm 2.45	20.05
LL	28.60 \pm 6.90	24.13	23.53 \pm 6.16	26.18	25.41 \pm 6.78	26.68
CL	208.10 \pm 41.02	19.71	188.00 \pm 41.24	21.94	195.44 \pm 41.56	21.27
CW	157.00 \pm 30.24	19.26	171.35 \pm 42.95	54.25	166.04 \pm 75.38	45.40
CH	92.80 \pm 17.78	19.16	96.00 \pm 56.28	58.63	94.81 \pm 45.40	47.88
V2L	42.60 \pm 6.08	14.27	44.65 \pm 14.85	33.28	43.89 \pm 12.23	27.87
V2W	60.00 \pm 10.35	17.25	54.29 \pm 10.50	19.34	56.41 \pm 10.62	18.82
V4L	47.00 \pm 10.03	21.34	42.00 \pm 9.30	22.14	43.85 \pm 9.70	22.12
V4W	58.60 \pm 11.52	19.66	56.00 \pm 11.81	21.07	57.00 \pm 11.55	20.26
DPW	35.20 \pm 8.36	23.75	30.82 \pm 6.77	21.97	32.44 \pm 7.55	23.27
VPW	18.60 \pm 4.60	24.73	11.59 \pm 5.15	44.44	14.19 \pm 5.96	42.00
LPY	27.00 \pm 6.78	25.11	21.53 \pm 6.58	30.56	23.56 \pm 7.06	29.97
AW	16.60 \pm 3.63	21.87	16.71 \pm 5.14	30.76	16.67 \pm 4.57	27.41
VW	32.50 \pm 11.37	34.98	35.12 \pm 12.67	36.08	34.15 \pm 12.05	35.29
S1L	29.30 \pm 7.90	26.96	29.65 \pm 15.01	50.62	29.52 \pm 12.66	42.89
S2L	19.40 \pm 7.11	36.65	15.76 \pm 6.45	40.93	17.11 \pm 6.80	39.74
S2W	35.80 \pm 12.65	35.34	34.18 \pm 17.67	51.70	34.78 \pm 15.75	45.29
ANBW	36.60 \pm 9.99	27.30	36.94 \pm 15.54	42.07	36.81 \pm 13.54	36.78
NBW	49.70 \pm 9.36	18.83	44.24 \pm 9.08	20.52	46.26 \pm 9.40	20.32
NBL	37.00 \pm 8.45	22.84	32.88 \pm 12.74	38.75	34.41 \pm 11.35	32.98
NL	17.70 \pm 28.84	162.94	10.71 \pm 10.27	95.89	13.30 \pm 19.09	143.53
N	10.90 \pm 5.04	46.24	15.88 \pm 17.12	107.81	14.04 \pm 13.97	99.50
PP ₃	38.60 \pm 5.25	18.36	26.41 \pm 5.30	20.06	27.22 \pm 5.29	19.43
DP ₃	9.00 \pm 4.69	52.11	12.76 \pm 13.09	102.59	11.37 \pm 10.80	94.99
LP ₃	64.80 \pm 11.01	16.99	58.06 \pm 13.89	23.92	60.56 \pm 13.10	21.63

¹See Figs. 25-28 for abbreviations.

TABLE 11 (CONTINUED). SHELL STATISTICS, *Gopherus berlandieri*.

Measure- ments ¹	Males (N=17)		Females (N=25)		Combined (N=42)	
	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV
PL	147.75 \pm 24.05	16.28	112.00 \pm 16.72	14.93	132.43 \pm 27.54	20.30
G	28.92 \pm 6.11	21.13	20.89 \pm 3.06	14.65	25.48 \pm 6.39	25.08
H	32.00 \pm 6.62	20.69	23.33 \pm 3.20	13.72	28.29 \pm 6.89	24.36
P	12.50 \pm 3.42	27.36	12.11 \pm 3.02	24.94	12.33 \pm 3.18	25.79
AB	45.83 \pm 9.02	19.68	35.56 \pm 6.39	17.97	41.43 \pm 9.39	22.67
F	22.17 \pm 4.02	18.13	18.44 \pm 4.00	21.69	20.57 \pm 4.34	21.10
A	13.33 \pm 3.47	12.00	9.00 \pm 1.73	19.22	11.48 \pm 3.56	31.01
ND	11.00 \pm 3.77	34.27	6.67 \pm 1.73	25.94	9.14 \pm 3.72	40.70
NW	19.17 \pm 4.93	25.72	12.33 \pm 3.35	27.17	16.24 \pm 5.47	33.68
XH	11.50 \pm 2.91	25.30	6.44 \pm 1.74	27.02	9.33 \pm 3.53	37.83
XL	32.25 \pm 4.49	13.92	25.56 \pm 5.22	20.42	29.38 \pm 5.79	19.71
XW	38.42 \pm 5.58	14.52	29.22 \pm 5.29	18.10	34.48 \pm 7.08	20.53
POL	38.67 \pm 14.28	36.93	32.56 \pm 4.69	14.34	36.05 \pm 11.43	31.71
HYP	29.83 \pm 5.72	19.18	23.33 \pm 2.92	12.52	27.05 \pm 5.68	21.00
HYO	34.17 \pm 6.06	17.73	29.11 \pm 6.53	22.43	32.00 \pm 6.62	20.69
EL	32.92 \pm 6.44	19.56	25.44 \pm 3.43	13.48	29.71 \pm 6.47	21.78
EW	29.67 \pm 6.05	20.39	22.44 \pm 4.69	20.40	26.57 \pm 6.51	24.50
ME	21.33 \pm 7.10	33.29	13.00 \pm 2.35	18.08	17.76 \pm 6.91	39.91
GE	36.33 \pm 7.16	19.70	25.44 \pm 4.50	17.69	31.67 \pm 8.18	25.83
AL	53.33 \pm 10.21	19.14	36.00 \pm 5.74	15.95	45.90 \pm 12.16	26.49
LT	14.50 \pm 2.61	18.00	10.11 \pm 2.09	20.67	12.62 \pm 3.23	25.59
LL	23.33 \pm 4.81	20.62	15.89 \pm 2.20	13.85	20.14 \pm 5.38	26.71
CL	152.33 \pm 23.74	15.58	120.22 \pm 17.48	14.54	138.57 \pm 26.41	19.06
CW	134.33 \pm 17.06	12.70	103.00 \pm 16.42	15.94	120.90 \pm 22.81	18.87
CH	84.42 \pm 16.87	2.00	62.67 \pm 12.09	1.92	75.10 \pm 18.35	24.43
V2L	32.83 \pm 4.15	12.64	26.89 \pm 2.98	11.08	30.29 \pm 4.70	15.52
V2W	51.33 \pm 7.40	14.42	40.33 \pm 4.53	11.23	46.62 \pm 8.33	17.68
V4L	39.83 \pm 5.57	13.98	30.89 \pm 4.34	14.04	36.00 \pm 6.72	18.67
V4W	51.92 \pm 8.87	17.08	39.78 \pm 5.43	13.65	46.71 \pm 9.64	20.64
DPW	31.25 \pm 5.61	17.95	20.56 \pm 8.50	41.34	26.67 \pm 8.70	32.62
VPW	12.83 \pm 7.41	57.76	9.78 \pm 3.90	39.88	11.52 \pm 6.22	53.99
LPY	21.92 \pm 4.96	22.63	12.67 \pm 5.70	44.99	17.95 \pm 6.97	58.83
AW	13.33 \pm 4.64	34.81	12.78 \pm 4.99	39.05	13.10 \pm 4.68	35.73
VW	32.08 \pm 7.20	22.44	23.56 \pm 9.63	40.87	28.43 \pm 9.18	32.29
S1L	28.33 \pm 10.47	36.96	18.78 \pm 8.38	44.62	24.24 \pm 10.58	43.65
S2L	113.50 \pm 4.93	36.53	9.11 \pm 4.04	44.35	11.62 \pm 4.98	42.86
S2W	33.92 \pm 9.19	27.09	20.67 \pm 9.46	45.77	28.24 \pm 11.29	39.79
ANBW	25.08 \pm 9.52	37.96	22.33 \pm 3.08	13.79	23.90 \pm 7.46	31.21
NBW	37.17 \pm 13.09	35.22	31.78 \pm 4.29	13.50	34.86 \pm 10.44	29.95
NBL	27.83 \pm 9.92	35.64	22.78 \pm 3.31	14.53	25.67 \pm 8.06	31.40
NL	2.42 \pm 1.88	77.69	2.89 \pm 1.62	56.06	2.62 \pm 1.75	66.70
N	6.75 \pm 3.62	53.63	5.89 \pm 2.57	43.63	6.38 \pm 3.17	49.69
PP ₃	21.42 \pm 7.12	33.24	17.89 \pm 7.74	43.26	19.90 \pm 7.42	37.29
DP ₃	4.17 \pm 2.12	50.84	2.67 \pm 2.55	99.51	3.52 \pm 2.38	67.14
LP ₃	54.25 \pm 8.95	16.50	39.22 \pm 15.16	38.65	47.81 \pm 13.93	29.14

¹See Figs. 25-26 for abbreviations.

TABLE 11 (CONTINUED). SHELL STATISTICS, *Gopherus flavomarginatus*.

Measure- ments ¹	Males (N=31)		Females (N=23)		Combined (N=54)	
	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV
PL	263.50 \pm 31.05	11.78	258.00 \pm 33.01	12.79	261.67 \pm 41.01	15.67
G	57.50 \pm 4.95	8.61	61.03 \pm 5.91	9.68	58.63 \pm 8.03	13.70
H	43.50 \pm 3.54	8.14	41.00 \pm 4.62	11.28	42.76 \pm 4.76	11.13
P	25.00 \pm 4.41	17.64	29.03 \pm 5.03	17.33	26.30 \pm 6.75	25.67
AB	73.00 \pm 10.83	14.83	67.06 \pm 9.81	14.63	71.12 \pm 17.75	24.95
F	43.00 \pm 6.01	13.98	41.00 \pm 5.32	12.99	42.33 \pm 6.80	16.06
A	26.01 \pm 4.30	16.53	22.61 \pm 8.31	41.18	24.67 \pm 10.68	43.29
ND	17.50 \pm 3.12	17.83	22.00 \pm 5.63	25.59	19.01 \pm 6.17	32.46
NW	27.50 \pm 14.95	54.36	26.81 \pm 12.01	44.80	27.13 \pm 15.61	57.54
XH	11.50 \pm 3.71	23.56	11.61 \pm 3.06	26.64	11.33 \pm 3.58	31.60
XL	62.00 \pm 8.41	13.56	56.00 \pm 9.03	16.13	60.17 \pm 10.61	17.63
XW	65.50 \pm 8.12	12.40	74.06 \pm 10.21	13.79	68.37 \pm 11.37	16.63
POL	86.50 \pm 8.12	9.39	79.00 \pm 9.63	12.19	84.92 \pm 10.58	12.45
HYP	48.50 \pm 9.16	18.89	45.00 \pm 10.18	22.62	47.38 \pm 9.92	20.94
HYO	66.00 \pm 9.28	14.06	67.00 \pm 10.00	14.93	68.18 \pm 13.06	19.16
EL	52.00 \pm 7.24	13.94	50.13 \pm 8.31	16.58	51.86 \pm 9.63	18.57
EW	51.50 \pm 7.12	13.83	46.86 \pm 7.33	15.64	49.57 \pm 8.51	17.17
ME	41.00 \pm 8.63	21.05	42.91 \pm 8.38	19.63	41.11 \pm 9.42	22.91
GE	58.00 \pm 9.41	16.22	63.61 \pm 9.38	14.75	59.13 \pm 10.06	17.01
AL	89.00 \pm 17.07	19.18	91.03 \pm 15.09	16.58	89.91 \pm 18.13	20.16
LT	17.00 \pm 6.16	36.24	22.66 \pm 8.14	35.92	18.17 \pm 9.33	51.34
LL	34.00 \pm 5.41	15.91	34.16 \pm 6.33	18.53	34.17 \pm 8.19	23.39
CL	288.00 \pm 61.09	21.21	268.16 \pm 58.13	22.22	281.33 \pm 63.19	22.46
CW	238.50 \pm 31.19	13.08	233.03 \pm 29.61	12.71	236.51 \pm 33.07	13.98
CH	130.26 \pm 28.15	21.23	145.06 \pm 27.51	18.96	138.66 \pm 38.18	27.53
V2L	55.50 \pm 8.63	15.55	52.16 \pm 8.96	17.18	54.39 \pm 10.15	18.47
V2W	95.61 \pm 10.12	10.58	96.21 \pm 9.68	10.06	95.76 \pm 12.61	13.17
V4L	68.91 \pm 10.77	15.63	68.03 \pm 10.93	16.07	69.71 \pm 15.56	22.32
V4W	98.00 \pm 10.03	10.23	95.28 \pm 9.13	9.58	97.03 \pm 11.63	11.99
DPW	52.19 \pm 4.24	8.12	54.43 \pm 5.30	9.74	52.67 \pm 6.31	11.98
VPW	24.62 \pm 6.41	26.04	27.23 \pm 5.01	18.40	25.28 \pm 8.45	33.43
LPY	36.00 \pm 5.71	15.86	38.51 \pm 6.63	17.22	36.78 \pm 8.92	24.25
AW	22.51 \pm 3.66	16.26	25.68 \pm 4.34	16.70	23.81 \pm 6.03	25.33
VW	74.63 \pm 10.13	13.57	69.31 \pm 9.10	13.21	63.93 \pm 19.07	29.83
S1L	52.01 \pm 12.41	23.86	49.93 \pm 18.42	36.89	57.83 \pm 21.16	36.59
S2L	32.50 \pm 8.77	26.99	31.00 \pm 9.91	31.97	32.48 \pm 10.07	31.00
S2W	56.88 \pm 9.51	16.72	60.91 \pm 10.15	16.66	57.83 \pm 12.73	22.36
ANBW	54.50 \pm 6.41	11.76	67.36 \pm 8.91	13.23	58.67 \pm 9.98	17.01
NBW	73.21 \pm 7.12	9.73	79.01 \pm 8.68	10.99	75.06 \pm 9.16	12.20
NBL	50.00 \pm 6.83	13.66	45.13 \pm 8.73	19.34	48.33 \pm 10.03	20.75
NL	12.53 \pm 3.71	29.60	10.13 \pm 2.82	27.84	11.67 \pm 5.53	47.38
N	21.01 \pm 3.96	18.85	17.62 \pm 3.17	18.00	19.78 \pm 5.69	28.77
PP ₃	40.38 \pm 4.91	12.16	45.51 \pm 3.01	6.61	41.07 \pm 5.06	12.32
DP ₃	9.03 \pm 1.41	15.61	4.93 \pm 2.61	52.94	7.83 \pm 3.09	39.46
LP ₃	89.51 \pm 10.17	11.36	95.89 \pm 13.07	13.63	91.02 \pm 15.81	17.37

¹See Figs. 25-26 for abbreviations.

TABLE 11 (CONTINUED). SHELL STATISTICS, *Gopherus polyphemus*.

Measure- ments ¹	Males (N=28)		Females (N=35)		Combined (N=63)	
	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV	$\bar{X} \pm SD$	CV
PL	228.95 \pm 27.05	11.82	218.70 \pm 42.40	19.39	217.00 \pm 51.99	23.87
G	37.85 \pm 8.19	4.62	30.40 \pm 12.42	42.50	35.48 \pm 10.31	29.06
H	40.10 \pm 5.69	14.20	42.20 \pm 7.54	17.87	40.36 \pm 6.86	17.00
P	22.85 \pm 5.24	22.93	22.30 \pm 3.77	16.91	23.00 \pm 4.79	20.83
AB	77.60 \pm 12.97	16.71	77.80 \pm 17.53	22.53	77.48 \pm 14.43	18.62
F	38.70 \pm 5.59	14.44	35.60 \pm 5.19	14.58	37.61 \pm 6.24	16.59
A	14.45 \pm 3.30	22.83	14.90 \pm 4.43	29.73	14.82 \pm 3.68	24.90
ND	15.25 \pm 3.01	19.74	15.10 \pm 3.75	24.83	14.97 \pm 3.50	23.38
NW	24.85 \pm 4.26	17.14	21.40 \pm 5.23	24.44	23.45 \pm 4.96	21.15
XH	13.70 \pm 2.79	20.37	13.20 \pm 3.52	26.67	13.55 \pm 3.17	23.39
XL	45.95 \pm 6.74	14.67	45.20 \pm 7.66	16.95	45.64 \pm 7.21	15.80
XW	54.30 \pm 7.77	14.31	52.90 \pm 10.40	19.66	53.73 \pm 9.15	17.03
POL	64.55 \pm 7.83	12.13	61.30 \pm 11.11	18.12	64.06 \pm 11.31	17.60
HYP	49.00 \pm 9.34	19.06	48.90 \pm 8.12	16.60	49.45 \pm 9.12	18.44
HYO	65.80 \pm 9.19	13.97	63.20 \pm 12.18	19.27	64.79 \pm 10.51	16.22
EL	43.20 \pm 8.38	19.40	41.90 \pm 8.01	19.12	42.64 \pm 8.22	19.28
EW	48.15 \pm 7.58	15.74	45.70 \pm 11.11	24.31	47.61 \pm 9.41	19.76
ME	27.20 \pm 5.88	21.62	22.50 \pm 11.00	48.89	25.15 \pm 8.12	32.29
GE	48.55 \pm 8.89	18.31	41.10 \pm 18.12	44.90	45.97 \pm 12.74	27.71
AL	72.30 \pm 11.00	15.24	61.40 \pm 26.58	43.29	68.36 \pm 18.15	26.55
LT	18.10 \pm 5.17	28.56	15.80 \pm 7.11	45.00	17.55 \pm 5.85	33.33
LL	28.85 \pm 5.85	20.28	23.20 \pm 10.59	45.65	26.88 \pm 7.98	29.69
CL	233.75 \pm 63.92	27.35	194.40 \pm 110.52	56.59	214.70 \pm 89.26	41.58
CW	179.30 \pm 49.80	27.77	163.60 \pm 67.39	41.19	169.21 \pm 62.17	36.74
CH	101.15 \pm 28.24	27.92	90.80 \pm 37.81	41.64	94.82 \pm 34.90	36.81
V2L	51.05 \pm 8.14	16.95	44.30 \pm 17.31	39.07	47.21 \pm 14.63	30.99
V2W	75.05 \pm 9.63	12.83	67.70 \pm 27.72	40.95	70.24 \pm 21.55	30.68
V4L	55.70 \pm 8.77	15.76	48.20 \pm 20.53	42.59	51.73 \pm 16.78	32.44
V4W	73.60 \pm 10.03	13.63	64.10 \pm 27.40	42.75	68.42 \pm 22.50	31.42
DPW	36.10 \pm 5.14	14.24	34.50 \pm 8.53	24.72	34.33 \pm 9.09	26.48
VPW	19.15 \pm 6.56	34.26	19.40 \pm 5.08	26.19	18.82 \pm 6.85	36.40
LPY	25.90 \pm 5.00	19.31	25.80 \pm 9.70	37.60	25.24 \pm 8.40	33.28
AW	16.35 \pm 3.12	19.08	16.40 \pm 3.81	23.23	16.12 \pm 3.32	20.60
VW	43.60 \pm 9.95	22.82	34.10 \pm 14.96	43.87	40.55 \pm 12.73	31.39
S1L	34.50 \pm 11.62	33.68	27.40 \pm 14.32	52.26	32.52 \pm 12.53	38.53
S2L	21.60 \pm 4.33	20.00	19.40 \pm 5.30	27.32	20.06 \pm 5.92	29.51
S2W	47.40 \pm 8.52	17.97	41.90 \pm 12.61	30.10	43.67 \pm 13.42	30.73
ANBW	41.80 \pm 5.99	14.33	41.10 \pm 10.34	20.33	41.55 \pm 7.47	17.98
NBW	54.35 \pm 6.38	11.74	54.50 \pm 13.48	24.73	54.24 \pm 9.43	17.39
NBL	42.40 \pm 5.97	14.08	41.10 \pm 8.69	21.14	41.88 \pm 7.18	16.91
NL	10.80 \pm 2.17	20.09	11.10 \pm 3.60	35.14	10.82 \pm 2.64	24.40
N	12.85 \pm 3.41	26.54	13.90 \pm 3.21	23.09	13.18 \pm 3.29	24.96
PP ₃	35.30 \pm 3.96	11.22	35.10 \pm 6.67	19.00	35.00 \pm 5.36	15.31
DP ₃	15.25 \pm 3.58	23.48	15.80 \pm 5.92	37.47	15.24 \pm 4.63	30.38
LP ₃	76.25 \pm 9.97	13.08	74.00 \pm 16.47	22.26	75.06 \pm 12.56	16.73

¹See Figs. 25-26 for abbreviations.

ever, significant differences do occur between the sexes of the other three species, with males being less variable than females (*polyphemus* males $CV=19.98$, females 33.79; *flavomarginatus* males 28.02, females 32.03; *agassizi* males 31.15, females 43.01) (Table 12).

- 5) None of the species differ significantly from any other in total carapace variability (*berlandieri* $CV=34.53$, *polyphemus* $CV=28.33$, *agassizi* $CV=33.04$, *flavomarginatus* $CV=31.08$).
- 6) Patterns of character variances differ in each of the four extant species.

The correlation of size and sex was investigated by means of an analysis of plastral length variance (σ) of adult males and females in each population. This showed that the deviation of each sample is homogeneous and within expected limits. The results of Bartlett's test of Chi-Square ($DF=77$) strongly suggest ($F=24.1$) that the observed differences in intersexual plastral length variances are due to differences in the mean lengths alone, and not to the observed variability of the sexual subpopulations.

An identical analysis of carapace length variances in adult males and females of each population shows that in this instance the observed differences in carapace variances are not homogeneous, inasmuch as the variance in *polyphemus* females is much greater than any other sample. Females tend to be more variable in other shell characters as well (No. 4 of both plastral and carapace sections above).

Osteological studies normally make use of one of three comparative techniques: ratios, log-ratios, or actual measurements. To determine which of these techniques would be most discriminatory in adult *Gopherus* shells, a series of discrimination analyses were completed, utilizing a stepwise regression technique (BioMed 005, UCLA Med. Center). Two tests analyzing discrimination ability of different techniques were applied to one dependent variable and four (and in another case to 10) independent morphological variables of the xiphiplastron in three *Gopherus* species (Table 13). Still another technique test utilized the same

TABLE 13.—COMPARISON OF ANALYSIS TECHNIQUES.

	Ratios			Log-ratios			Measurements		
	C.D. ¹	D.D. ²	I.C. ³	C.D. ¹	D.D. ²	I.C. ³	C.D. ¹	D.D. ²	I.C. ³
4 INDEPENDENT VARIABLES									
<i>polyphemus</i> x <i>agassizi</i> (n=40)	11	21	14	14	23	3	18	16	2
<i>berlandieri</i> x <i>agassizi</i> (n=36)	6	30	0	7	29	0	32	4	0
<i>polyphemus</i> x <i>berlandieri</i> (n=38)	3	34	1	7	30	1	31	7	0
10 INDEPENDENT VARIABLES									
<i>polyphemus</i> x <i>agassizi</i> (n=40)	35	5	0	11	28	1	36	4	0
<i>polyphemus</i> x <i>berlandieri</i> (n=38)	19	8	11	17	1	20	21	8	9
<i>berlandieri</i> x <i>agassizi</i> (n=30)	14	11	5	10	2	18	27	3	0

¹C.D. = Correctly differentiated.

²D.D. = Doubtfully differentiated.

³I.D. = Incorrectly differentiated.

independent variables, combined the species, and used sex as the single dependent variable (Table 14). The results clearly show that, for adults, analyses based on log-ratio comparisons are less discriminatory than those using the actual measurements or ratios. The necessity of using variables with the same variances in ratio analyses, the danger of comparing dependent variables, and the fact that only adults were being studied, suggest using only actual measurements and a restricted suite of ratios as a basis of comparison throughout most of the remaining analyses.

TABLE 14.—COMPARISON OF ANALYSIS TECHNIQUES (4 Independent Variables, dependent variable sex [$n=57$]).

	Ratios	Log-ratios	Actual Measurements
Correct	15	9	13
Doubtful (with \pm probable error)	42	48	42
Clearly incorrect	0	0	2

The mean (\bar{X}), standard deviation (SD), and coefficient of variation (CV) of the measured characters were computed (Table 11). Each of the measurements was roughly plotted against plastral or carapace lengths to eliminate the problem of size differences and to estimate regression lines. Of the 46 possibly significant characters, 23 were concerned with carapace shape and 24 with plastron shape. The diagnostic value of each character in distinguishing a pair of species was tested by computing single character distances for the pair, and dividing the difference in means for the two populations by the average standard deviation.

From this analysis 5 carapace and 12 plastral measurements were found to be most diagnostic, although there was overlap between all species pairs in every character studied. These measurements, which were used in the linear discrimination tests, are: carapace length, carapace height, carapace width, distal and proximal widths of pleural 3; plastral length, xiphiplastron length and width, posterior lobe width, epiplastral lip thickness and length, epiplastral bone length and width, entoplastral length and width, and anterior lobe length and width.

The linear discrimination technique has been described and its use explained by Kendall (1951), Jolicoeur (1959), and Lawrence and Bosser (1967). Rao (1952) extended its usefulness through certain clustering statistics. The discrimination tests find the weighted sum of characters that best separates the populations (where the sum = the discrimi-

nant function DF, the weights = the discriminant coefficients DC, and the population mean of DF is the $\bar{DF} \times DC$ for each character). The relationship of tested population pairs depends on an evaluation of the DF separating the population pair. Population pairs that are most similar have similar DF values. The accuracy of the expression of relationship depends on the degree to which the populations are separated by DF. In addition, the multiple character difference between *Gopherus* species was also estimated using Mahalanobis' D^2 statistic, which is a general extension of distance comparisons for single characters. For this study the discriminant coefficients and the D^2 statistic for each pair of the selected populations of *Gopherus polyphemus*, *G. berlandieri*, *G. agassizi*, and *G. flavomarginatus* were computed using the 17 selected adult shell characters (Table 15). We see that *polyphemus* differs by 2.4 and 13.6 standard deviations from *flavomarginatus* and *berlandieri*, respectively, whereas *agassizi* and *berlandieri* differ by only 3.1 standard deviations. These tests serve to emphasize the separation of *Gopherus* into two major groups.

TABLE 15.—GENERALIZED D^2 DISTANCE (AND STANDARD DEVIATIONS) BETWEEN EXTANT POPULATIONS OF *Gopherus*.

	<i>agassizi</i>		
<i>polyphemus</i>	64.8 (08.3)	<i>polyphemus</i>	
<i>flavomarginatus</i>	55.8 (12.6)	8.1 (02.4)	<i>flavomarginatus</i>
<i>berlandieri</i>	21.3 (03.1)	82.3 (13.6)	92.7 (18.9)

The analysis of relationship was checked by tentatively assigning each specimen to one of the populations by use of the functions, and then checking each assignment *a posteriori* against the actual identification. With the proper choice of characters, most of the specimens can be correctly identified, though there is considerable overlap in species DF values. The results of these analyses are plotted in Figure 28. Although the results are less clear, *G. polyphemus* and *G. flavomarginatus* are closer to one another in both coordinates, whereas *berlandieri* is clearly different. *Gopherus agassizi* overlaps the characters of the remaining three species in both coordinates.

QUALITATIVE SPECIES-CORRELATED SHELL CHARACTERS.—To date most efforts to measure differences between the shells of *Gopherus* populations or to identify fossil specimens have used few specific measurements of any kind. They have relied mainly on size and general proportions. However, the overlap is so great that many individuals, particularly fos-

sils, cannot be reliably identified. Species characteristics of the shell depend on complex differential development of the component parts of the shell. In their extreme form, these differences are easily seen. In most cases, these are the characters upon which paleontological work depends, because large series of specimens from restricted sites are not available. Thus, from a practical standpoint, identifying fragmentary fossil specimens using multivariate analysis techniques is often impractical. Identifications must instead be based on a simple system, without resorting to the kind of analysis described above. The simplest system is usually a direct comparison of fossil shell fragments with the bones of known species.

Certain parts of the shell are quite diagnostic, and, when used in combination, will serve to identify most reasonably complete adult fossil specimens. A graphic summary of these general differences (which are usually best developed in adult males) between species of the genus *Gopherus* is provided in Figure 32. In identification of fossils, reference should also be made to shells of typical adults of all extant species (Figs. 29-32).

A short description of the salient differentiating characteristics of the shells of most adult specimens of each species follows. The quantitative parameters of the shells of extant populations of *Gopherus* are given in Table 12. Reference should also be made to appropriate figures in the text. In considering species-correlated characters it is important to reiterate that certain secondary sex characters are sometimes confused with specific characters. Thus, adult males of all species generally have a more concave plastron, the gular projection is proportionately longer, and the posterior xiphiplastral projection is thickened and directed more laterally, with more blunted tips than in adult females.

Qualitative shell characters found to be useful in separating the four extant species are:

1. Adjacent pleural bones (Figs 29-32) typically are alternately wider and narrower in almost all tortoises having high shells. This arrangement apparently strengthens the dome. As might be expected, it is best developed in *berlandieri*, in which the shell is proportionately higher than in the other species. This character is expressed in the ratio of the measurements: Distal width costal scute 3, Proximal width costal scute 3 (\bar{X} ratio: *berlandieri* = 5.65, \bar{CV} = 67.14; *agassizi* = 2.39, \bar{CV} = 94.99; *flavomarginatus* = 5.22, \bar{CV} = 28.31; *polyphemus* = 1.78, \bar{CV} = 30.38).

In *berlandieri* some pleurals actually fail to reach the peripherals. This character is most variable in *berlandieri* (\bar{CV} = 67.14) and *agassizi* (\bar{CV} = 94.99).

The pygal is generally more triangular in *berlandieri* than in the other species. *G. polyphemus* is broadest caudally (Fig. 33, I).

2. The keel on the bridge peripherals is best developed in *berlandieri*, most weakly developed in *polyphemus*, and intermediate in the other two species (Fig. 33, II).

3. The outward-shell flare over the hind legs is stronger in males than in females. Within each sex it tends to be best developed in *agassizi* and *berlandieri*, intermediate in *flavomarginatus*, and least developed in *polyphemus* (Fig. 33, III).

4. In males, the curve (as seen from above) formed by the posterior pleurals and suprapygal is broadly rounded in *polyphemus* and *flavomarginatus*, rounded to slightly angled in *agassizi*, and usually strongly angled in *berlandieri*. This is related to the degree of doming of the shell, the flaring over the hind legs, and the downward twisting of the posterior part of the carapace (Fig. 33, IV).

5. The shell height is proportionately highest in *G. berlandieri* ($CH/CL=1.84$), intermediate in *agassizi* ($\bar{X}=2.07$) and *flavomarginatus* ($\bar{X}=2.04$), and lowest in *polyphemus* ($\bar{X}=2.68$).

6. The highest part of the shell is usually behind the midpoint in *berlandieri*, usually at the middle in *agassizi*, and at the middle or anterior to it in *polyphemus* and *flavomarginatus*.

7. The widest part of the shell is usually well behind the center in *berlandieri*; behind the center, but less markedly so, in *agassizi*; center (sometimes behind it) in *flavomarginatus*; and also at the center, but with rather parallel sides, in *polyphemus*.

8. In both *berlandieri* and *agassizi*, the upper surface of the epiplastral lip is often concave. It is rarely so in *flavomarginatus* or *polyphemus*, particularly the latter. The lip is usually proportionately longer in *berlandieri* and *agassizi* (Fig. 33, VIII).

9. The bridge is shortest in *flavomarginatus* $\left(\frac{\text{Bridge L}}{\text{Plastron L}} \bar{X}=2.99 \right)$,

longest in *polyphemus* (2.57), and intermediate in *agassizi* (2.77) and *berlandieri* (2.67). The anterior and posterior plastral lobes are nearly equal in *polyphemus* (Ant. Lobe L/Plastral L $\bar{X}=3.25$, Post. Lobe L/Plastral L $\bar{X}=3.37$) and *flavomarginatus* (3.26 and 3.41), and more unequal in the two remaining species (*agassizi* 2.84 and 3.43; *berlandieri* 2.58 and 3.66 respectively). The bridge in *polyphemus* and *flavomarginatus* is almost always larger than both the anterior and the posterior lobes. In *agassizi* and *berlandieri* the bridge length usually equals the anterior lobe length and is larger than the posterior lobe (*polyphemus* Bridge

L/Plastral L. \bar{X} =2.57; *flavomarginatus* 2.99; *agassizi* 2.77; *berlandieri* 2.67) (Fig. 33, IX).

11. The entoplastron is very often narrow and long in *berlandieri* (Entoplastral L/Entopl. W \bar{X} =0.89), with the lateral apices of the pentagonally-shaped bone often in the anterior half. In the remaining species these apices are always in the posterior half. The element is usually widest in *polyphemus* (1.11), and intermediate in *flavomarginatus* (0.95) and *agassizi* (1.03) (Fig. 33, X).

12. In all adult tortoises, the periphoro-pleural articulation is completely fused, whereas in subadults this is not so. This fusion occurs at different sizes in each of the *Gopherus* species, and is obviously directly correlated with adult size attained by each of the species. In *berlandieri* fusion occurs at a shell length of about 130 mm, in *agassizi* about 180 mm, in *polyphemus* about 225 mm, and in *flavomarginatus* about 240 mm (Fig. 33, XI).

13. From the front, the anterior opening of the shell is more concave dorsally in *berlandieri* than in the remaining three species (Fig. 33, XII).

14. In adult males the epiplastral projection is narrowest and longest in *berlandieri*, and is often quite bifurcated. In *agassizi* it is quite variable, ranging from this extreme to a wide, medium-length process with a shallow notch. The projection in *polyphemus* is proportionately widest and shortest, is never bifurcate, and often lacks even the median anterior notch. *G. flavomarginatus* broadly overlaps the lower end of the range of variation in *agassizi* and overlaps almost the entire range of variation of *polyphemus* (Fig. 33, XIII).

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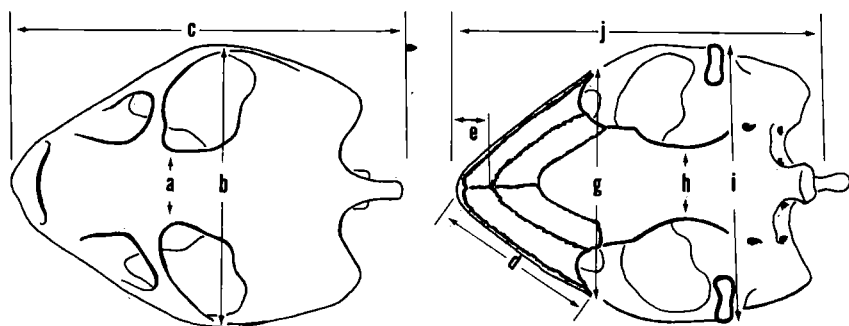


FIGURE 1.—Skull measurements utilized in this study. In addition, k = greatest skull height, f = outer alveolar angle.

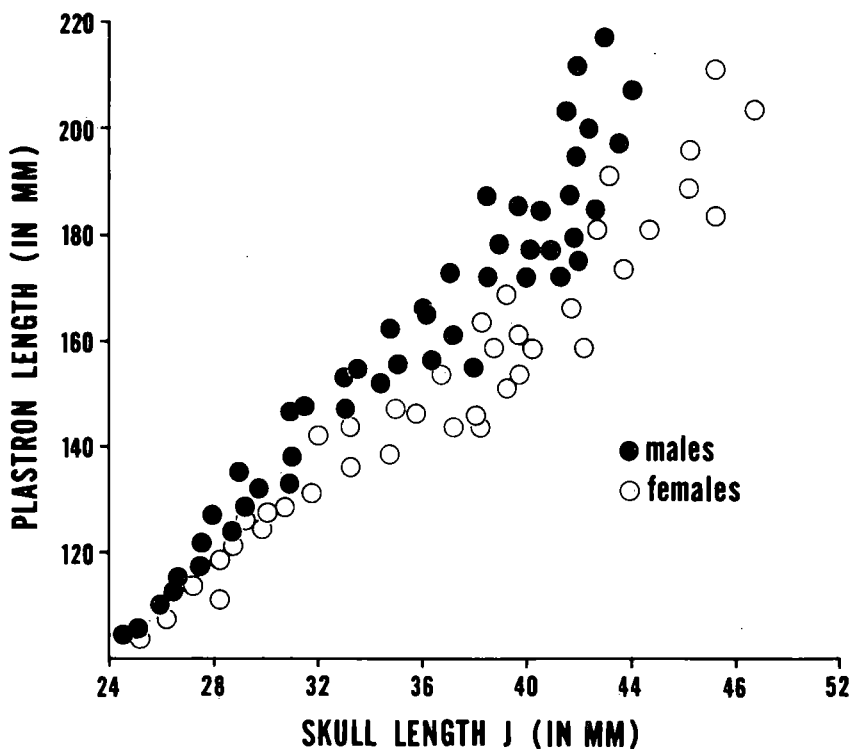


FIGURE 2.—The skulls of *Gopherus berlandieri* males are proportionately longer than those of females.

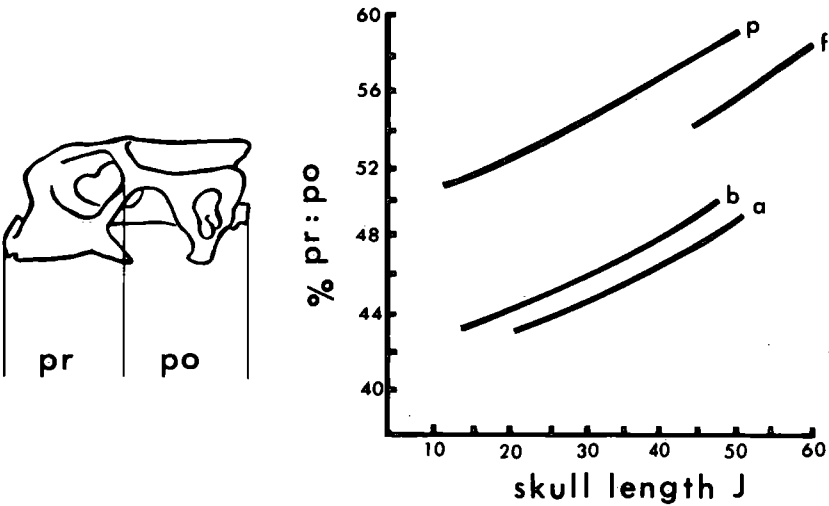


FIGURE 3.—During growth the preorbital area of the skull increases faster than the postorbital area. a = *agassizi*, b = *berlandieri*, f = *flavomarginatus*, p = *polyphemus*.

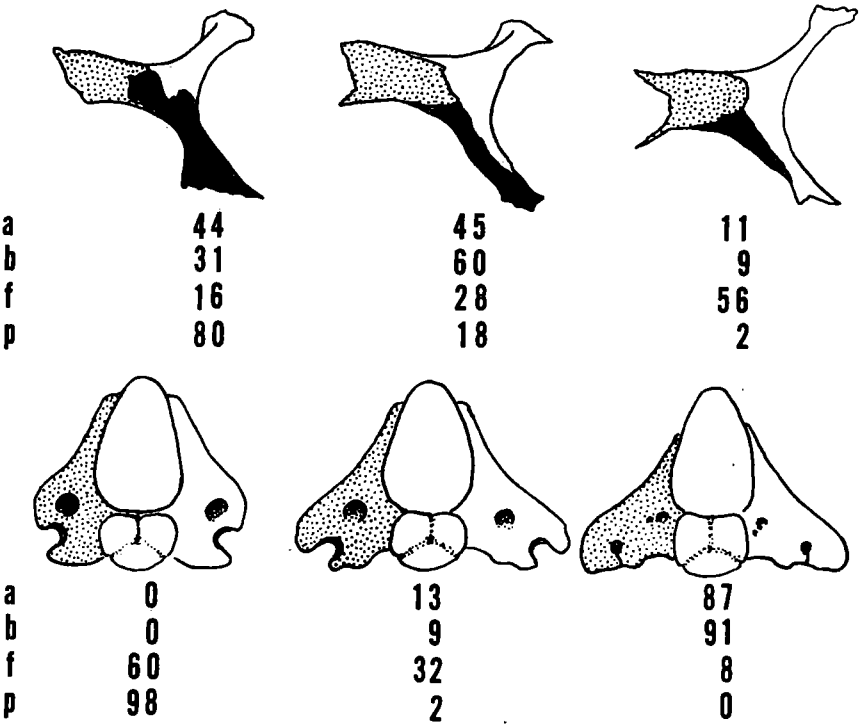


FIGURE 4.—Upper row, major bone patterns of the postorbital bar, clear = postorbital, black = jugal, stippled = quadratojugal. Lower row, patterns of exoccipital shape (stippled) and included foramina. a = *G. agassizi*, b = *G. berlandieri*, f = *G. flavo-marginatus*, and p = *G. polyphemus*.

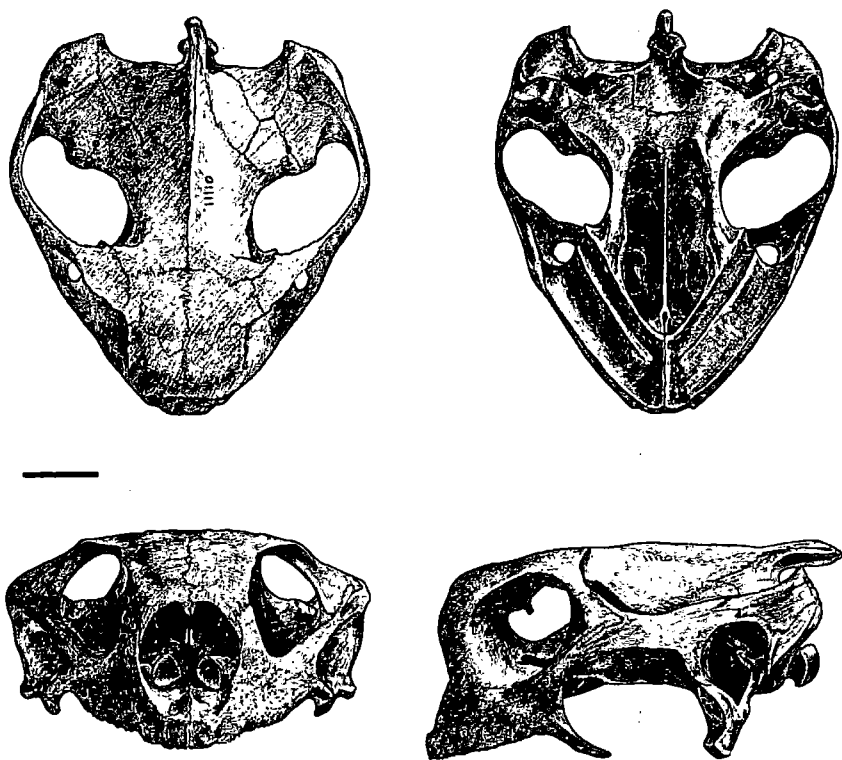


FIGURE 5.—Skull, *Gopherus polyphemus*, UF 11110.

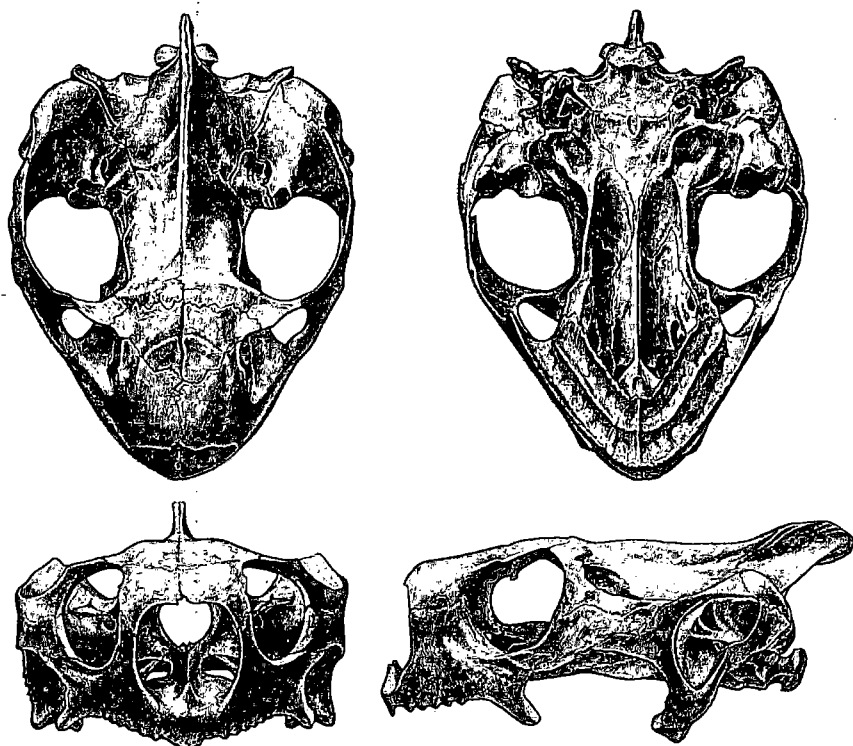


FIGURE 6.—Skull, *Gopherus agassizi*, W. A. Field No. 75.

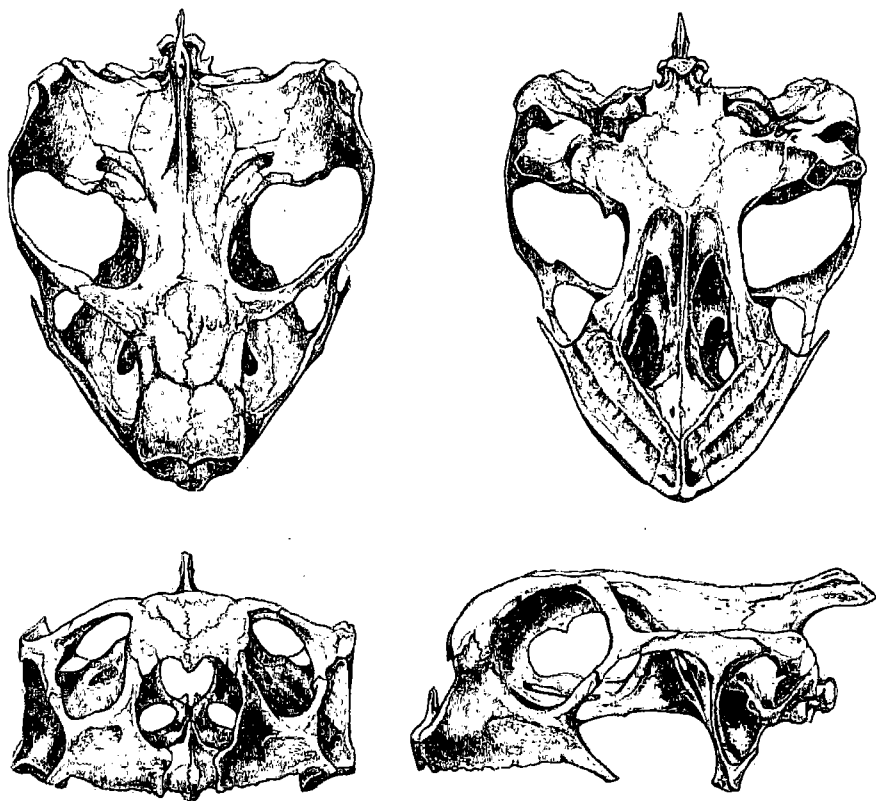


FIGURE 7.—Skull, *Gopherus flavomarginatus*, W. A. Field No. 200.

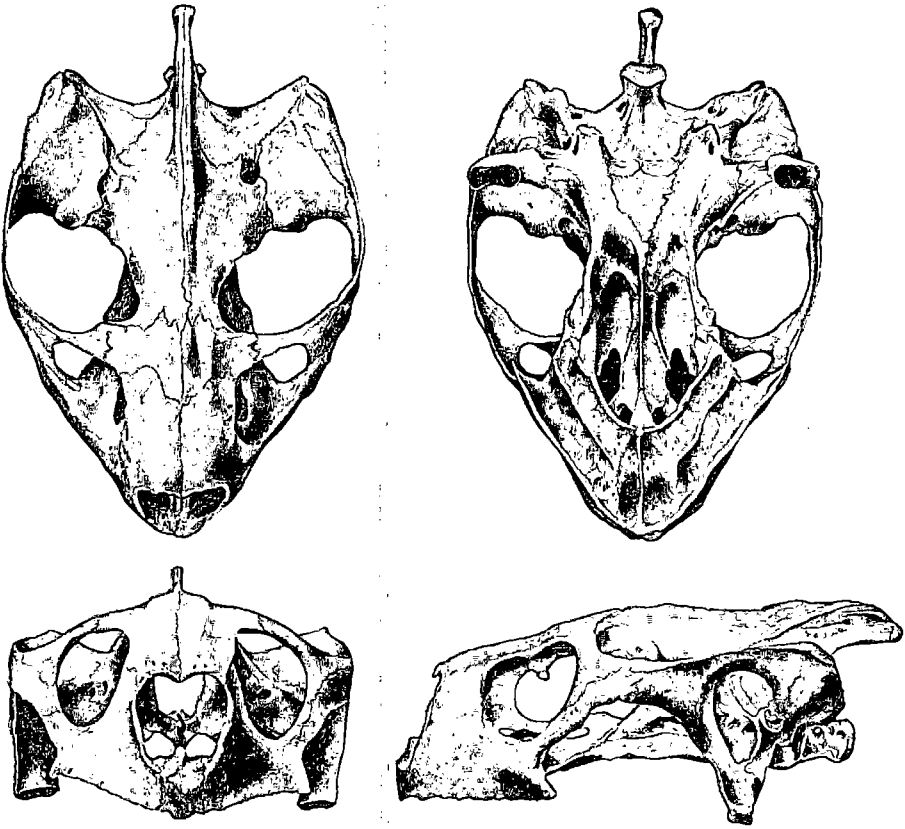


FIGURE 8.—Skull, *Gopherus berlandieri*, W. A. Field No. 21.

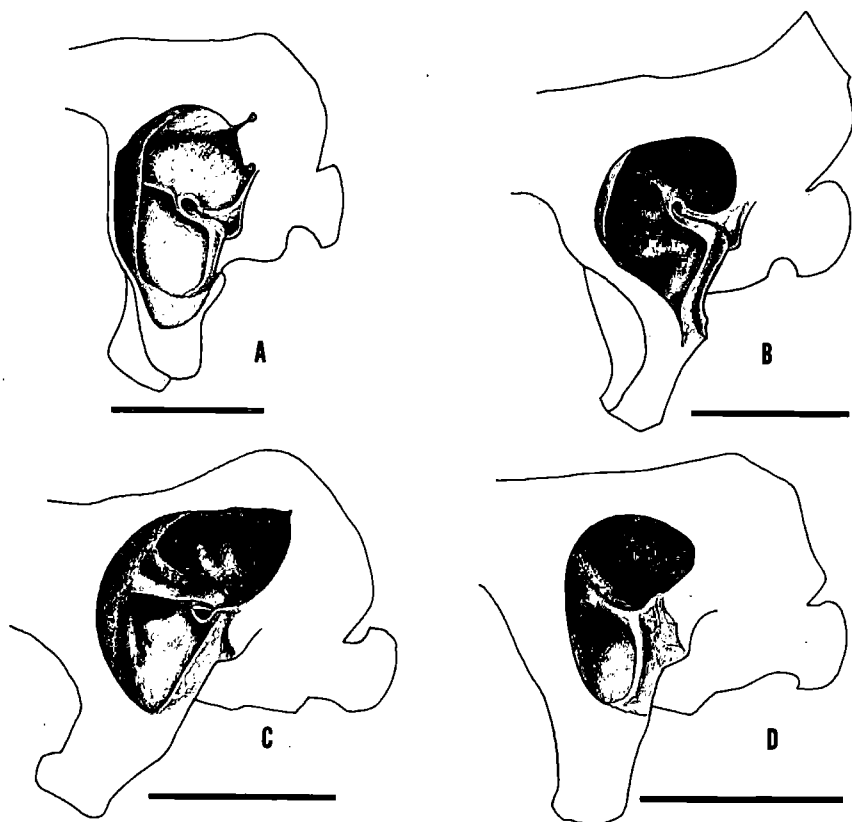


FIGURE 9.—Otic area, A. *Gopherus flavomarginatus*, B. *G. polyphemus*, C. *G. agassizi*, D. *G. berlandieri*. Bars represent 1 cm.

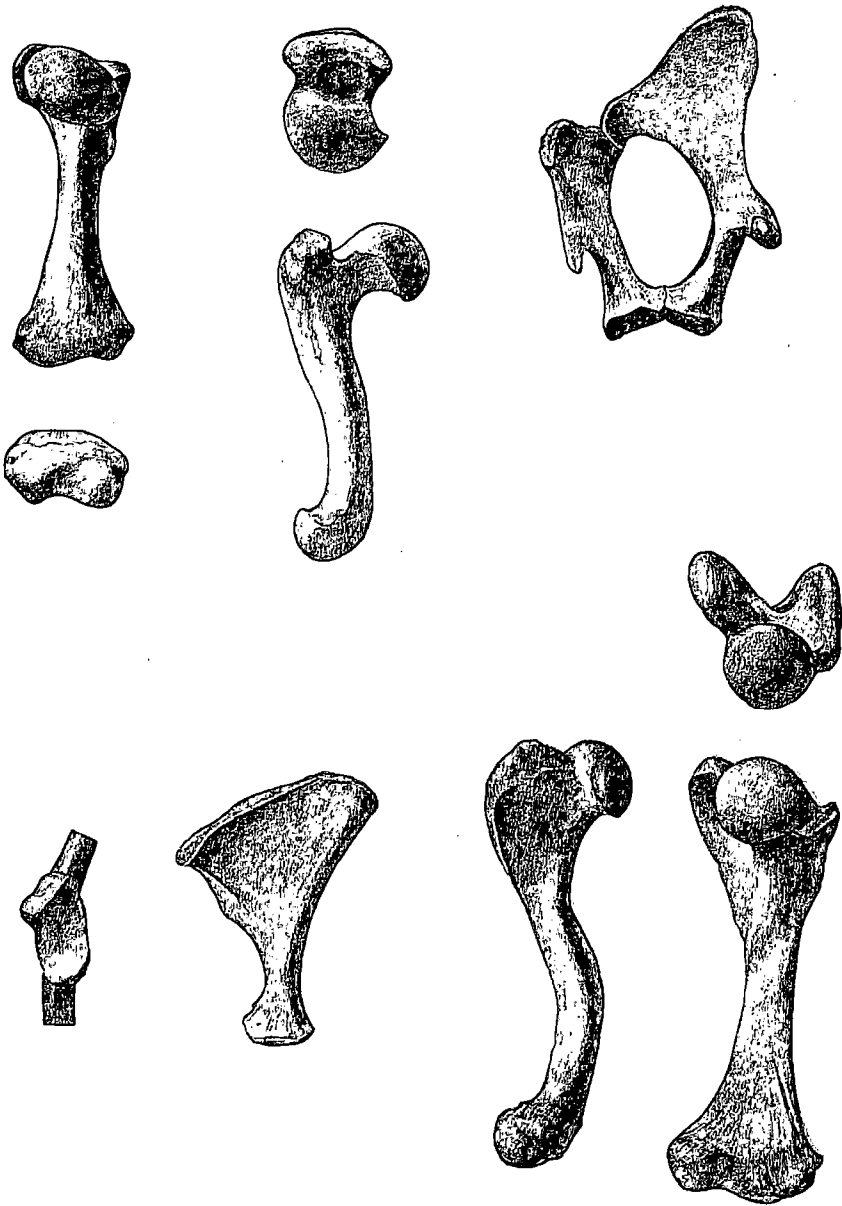


FIGURE 10.—Appendicular skeleton, *Gopherus polyphemus*, UF 11110. Upper left, femoral views; upper right, pelvis; lower left, scapular articulation and coracoid; lower right, humeral views.

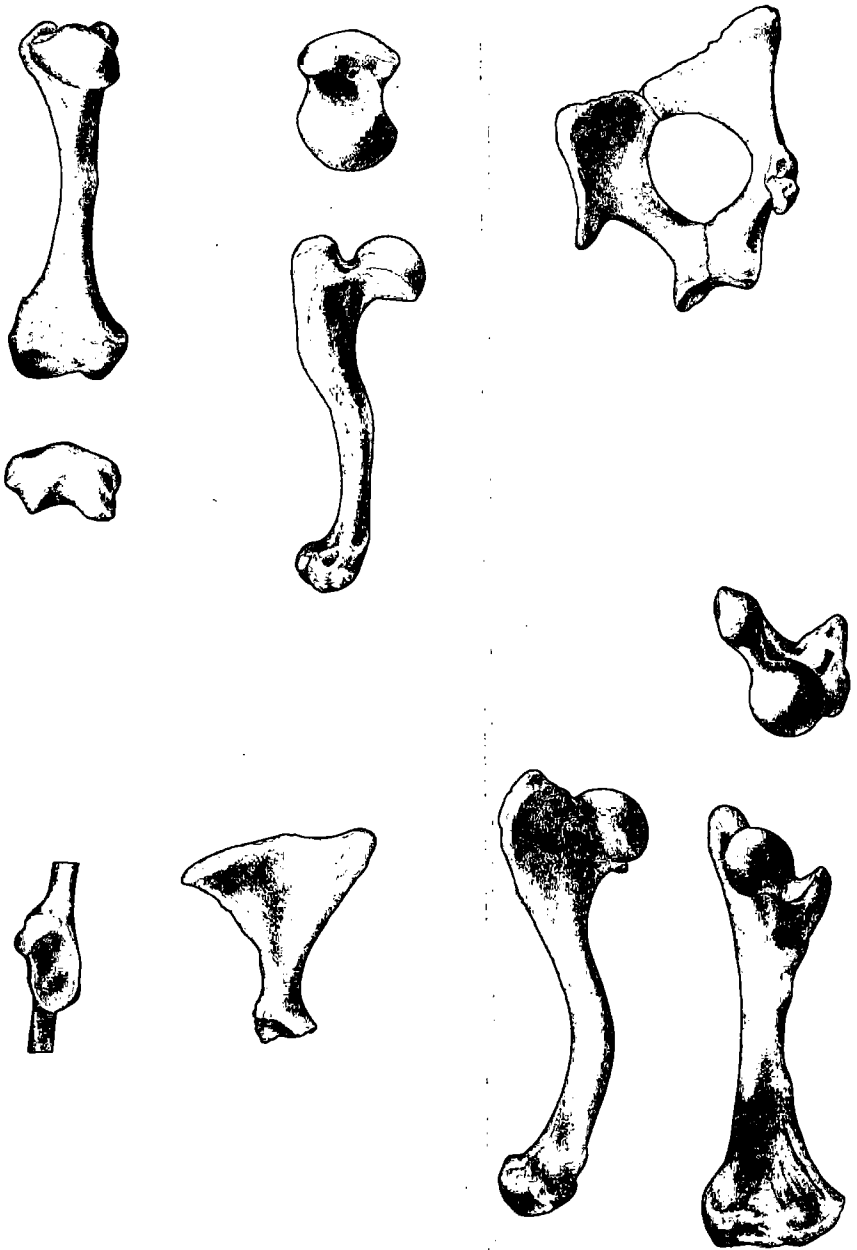


FIGURE 11.—Appendicular skeleton, *Gopherus berlandieri*, W. A. Field No. 21. Same views as Figure 10.



FIGURE 12.—Appendicular skeleton, *Gopherus flavomarginatus*, W. A. Field No. 63. Same views as Figure 10.

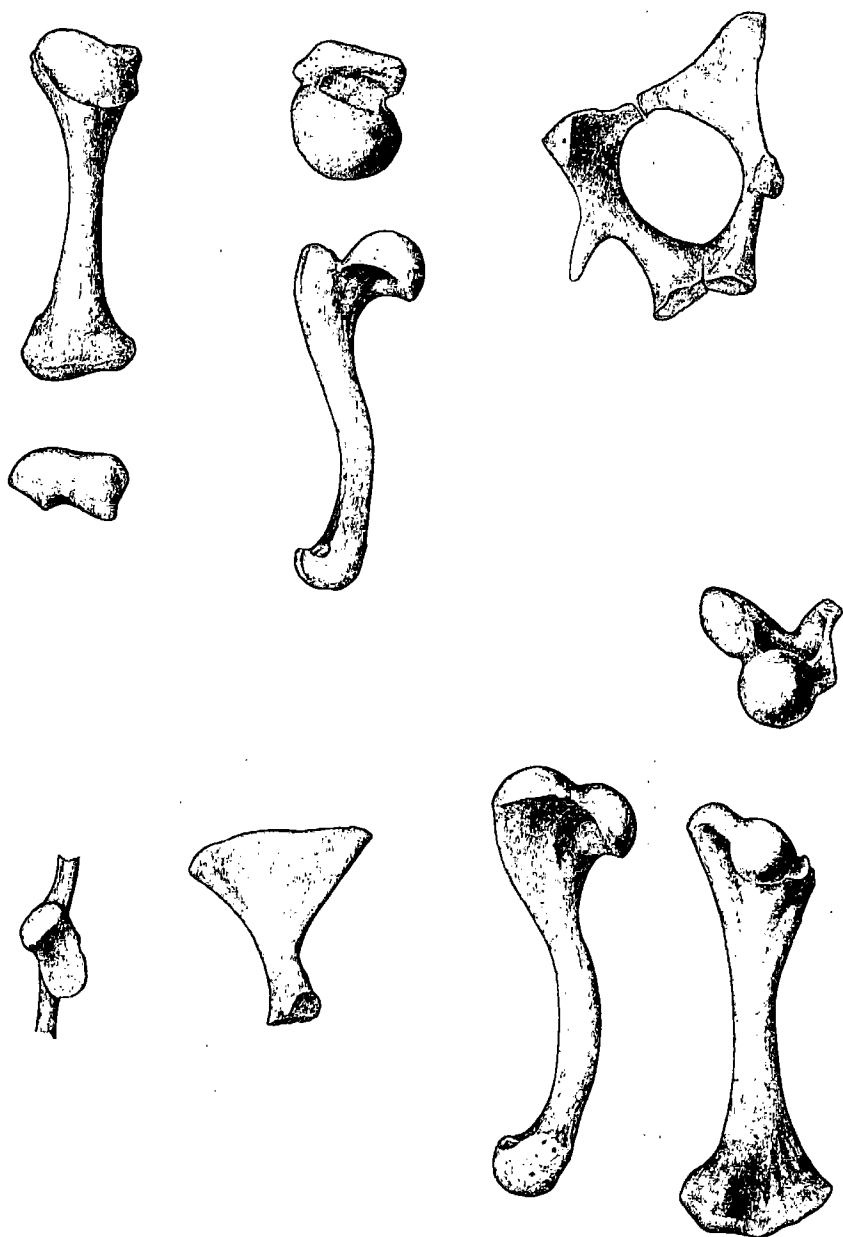


FIGURE 13.—Appendicular skeleton, *Gopherus agassizi*. W. A. Field No. 83. Same views as Figure 10.

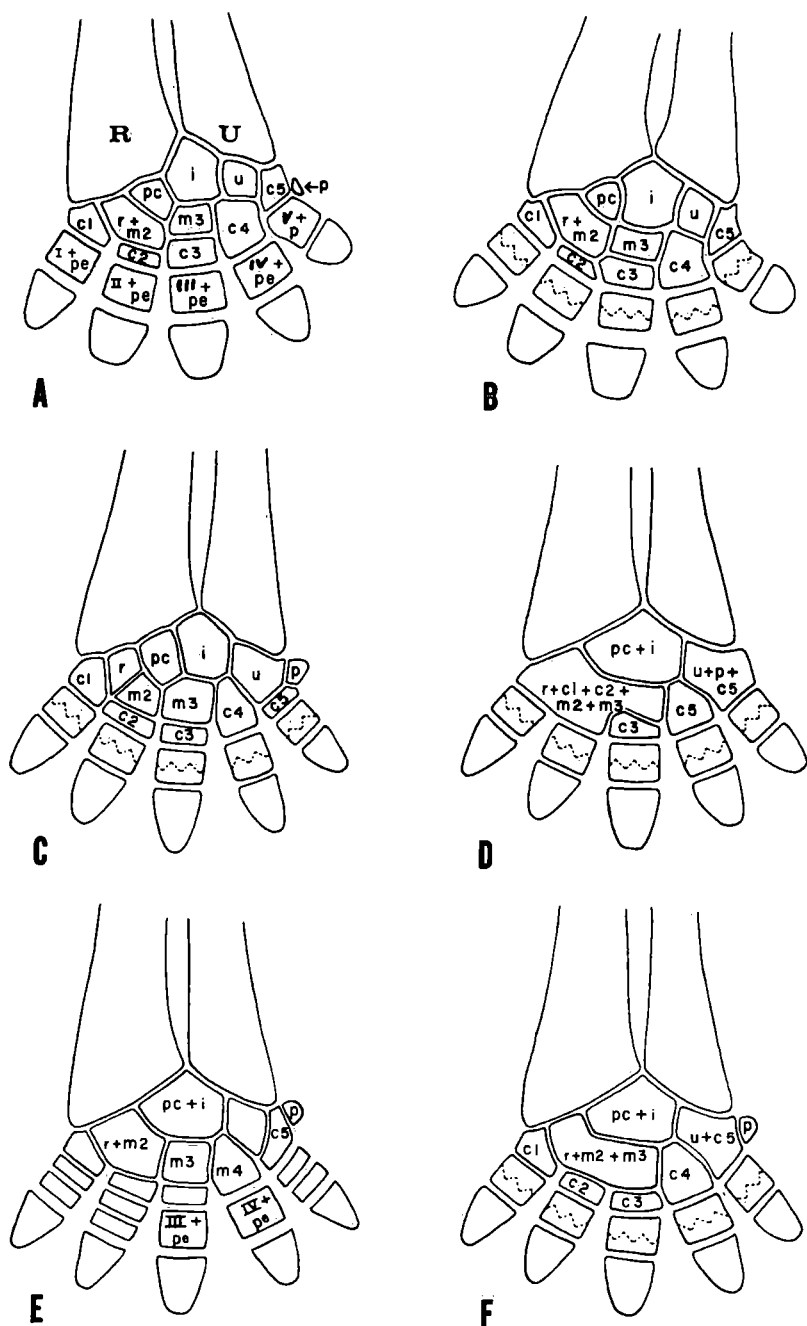


FIGURE 14.—Carpi (diagrammatic) of *Gopherus* species: A. Adult *G. polyphemus*, B. Adult *G. flavomarginatus*, C. Juvenile *G. agassizi*, D. Adult *G. agassizi*, E. Juvenile *G. berlandieri*, F. Adult *G. berlandieri*.

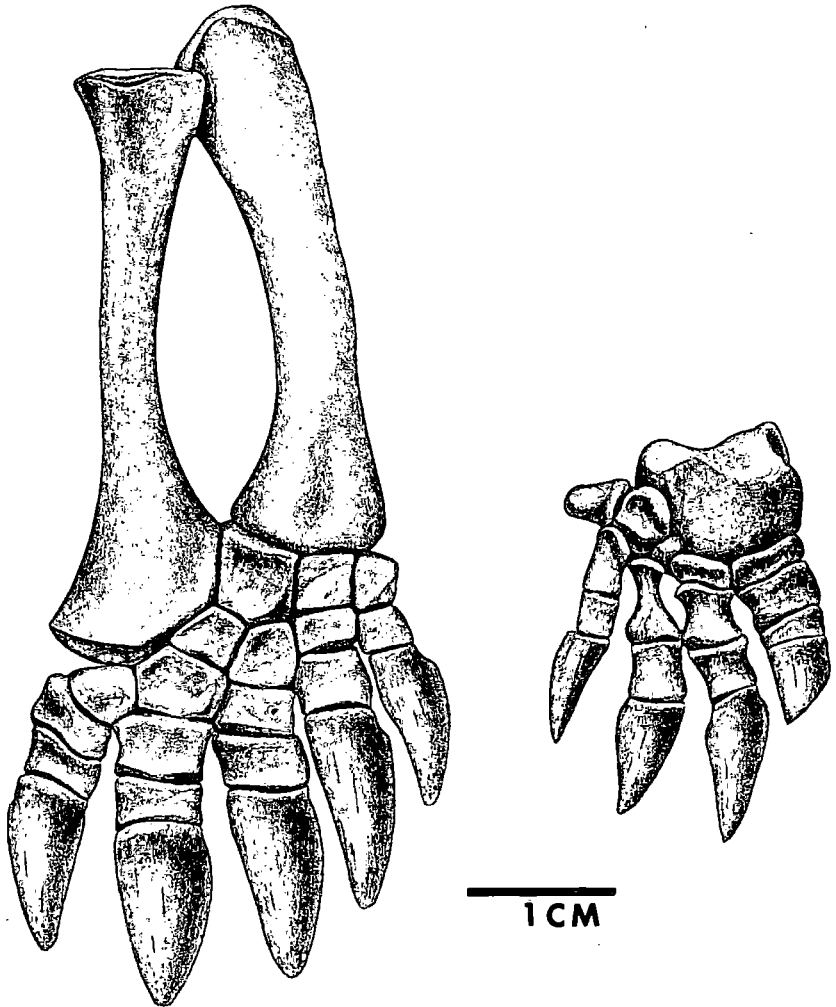


FIGURE 15.—Manus (left), and pes (right) of *Gopherus polyphemus*, UF 11110.

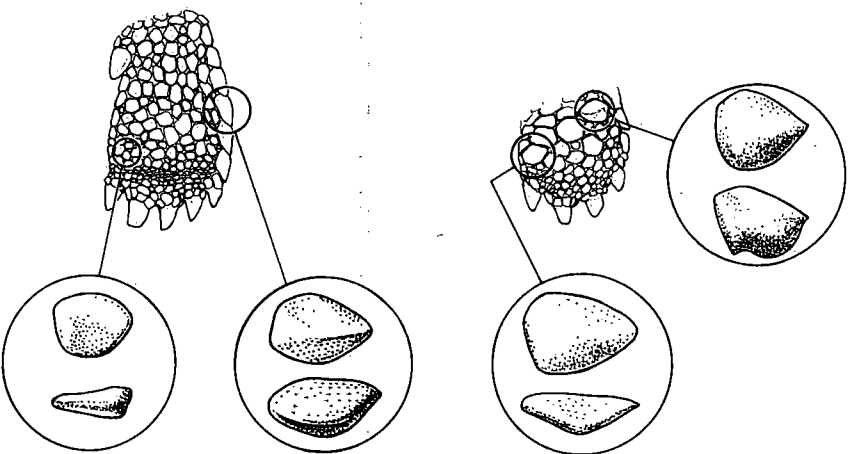


FIGURE 16.—Dermal armor of the outer surface of the manus (left) and heel of the pes (right) of *Gopherus polyphemus*.

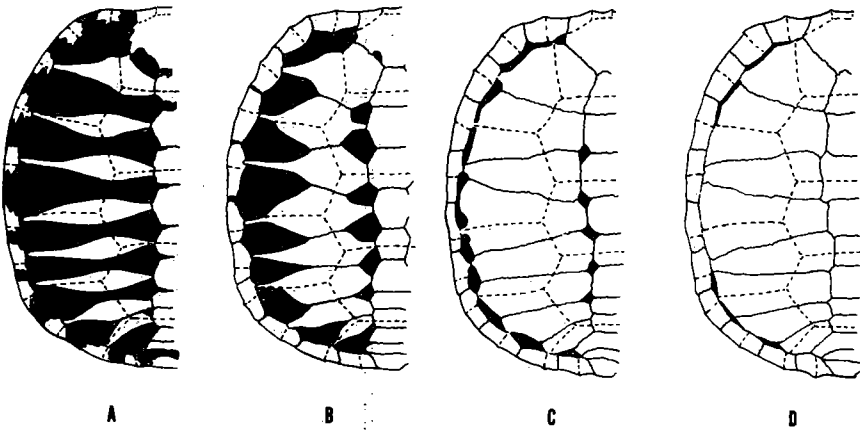


FIGURE 17.—Ossification of the carapace in *Gopherus polyphemus*. A) Shell length 72 mm; B) Shell length 109 mm; C) Shell length 182 mm; D) Shell length 204 mm.

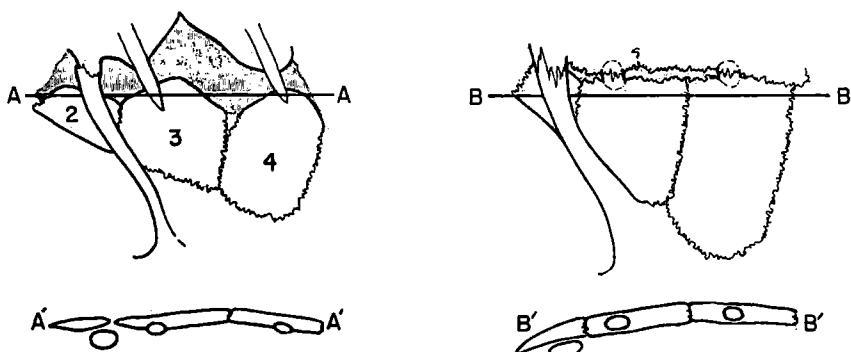


FIGURE 18.—Left, peripheral-pleural articulation in a young *Gopherus polyphemus* (W. A. Field No. 70), carapace length 127 mm. Upper, inner surface of anterior bridge peripherals (numbers 2-4), showing relationship of rib ends and peripherals. Lower, cross section through AA above showing rib ends in shallow peripheral grooves. Right, Same in a young adult *Gopherus polyphemus* (UF 10944), carapace length 171 mm. Rib ends are now in shallow peripheral pits.

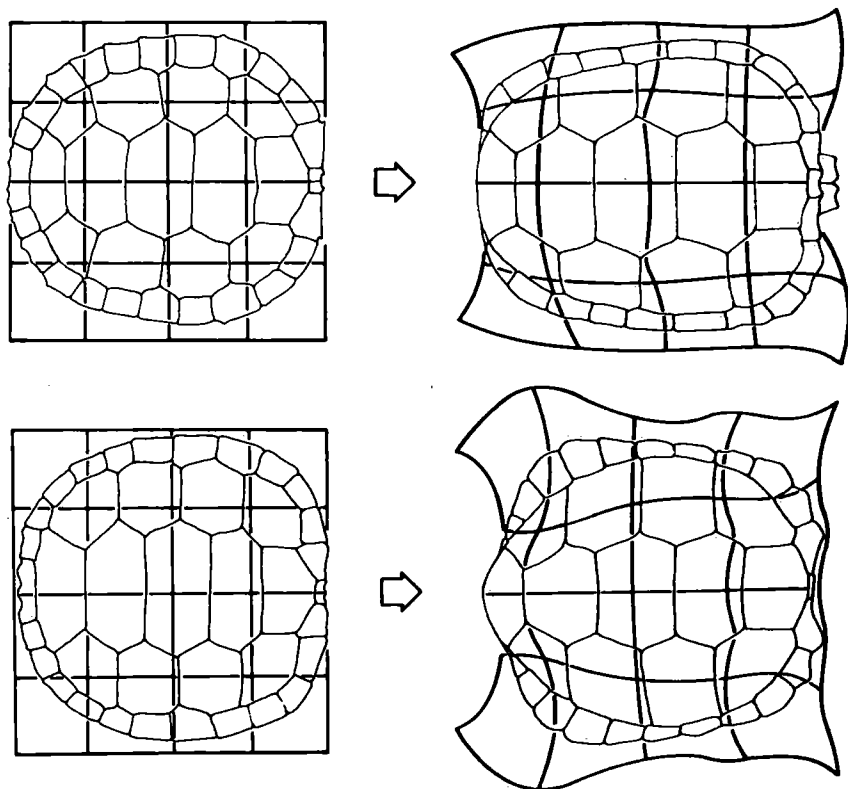


FIGURE 19.—Carapace growth patterns in, upper, *G. polyphemus*; lower, *G. berlandieri*. Hatching on left, adults on right.

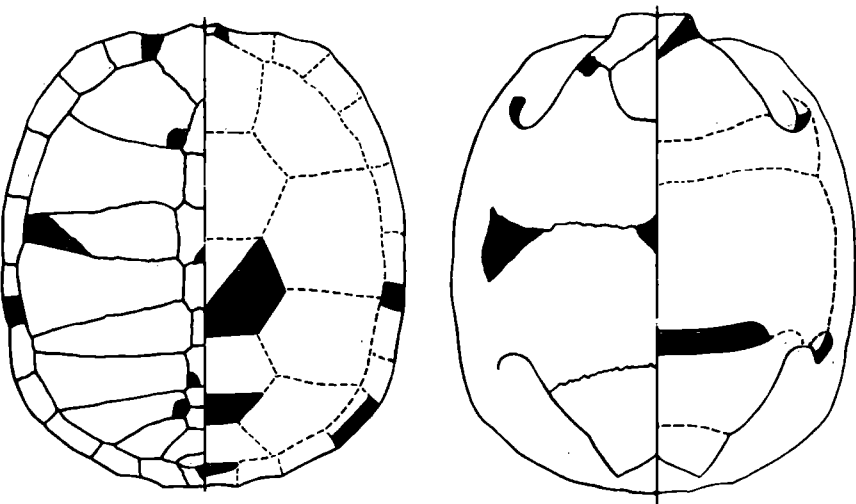


FIGURE 20.—Major types of anomalies recorded in the bones and scutes of *Gopherus* (all species combined). Bones are on the left of each figure, scutes on right.

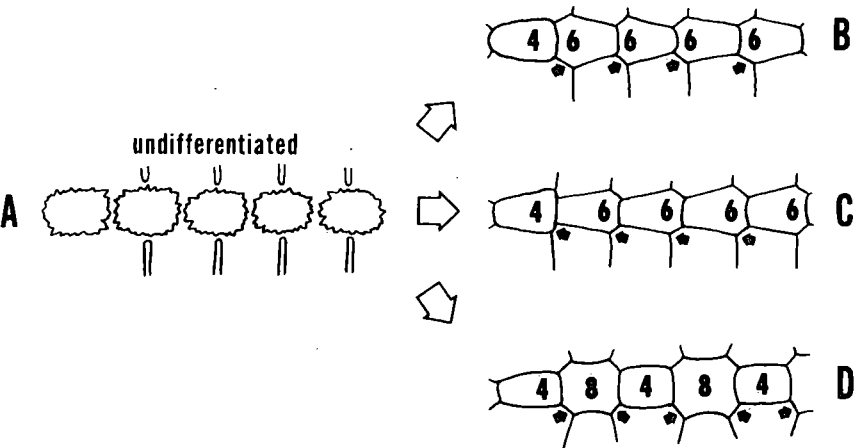


FIGURE 21.—Neural differentiation in turtles. Black arrows indicate major growth direction in pleural bones. A, undifferentiated pattern of most hatchling tortoises. B, typical neural pattern of most emydine turtles and primitive testudinines. C, pattern variant found in several turtle groups. D, typical pattern of advanced tortoise groups.

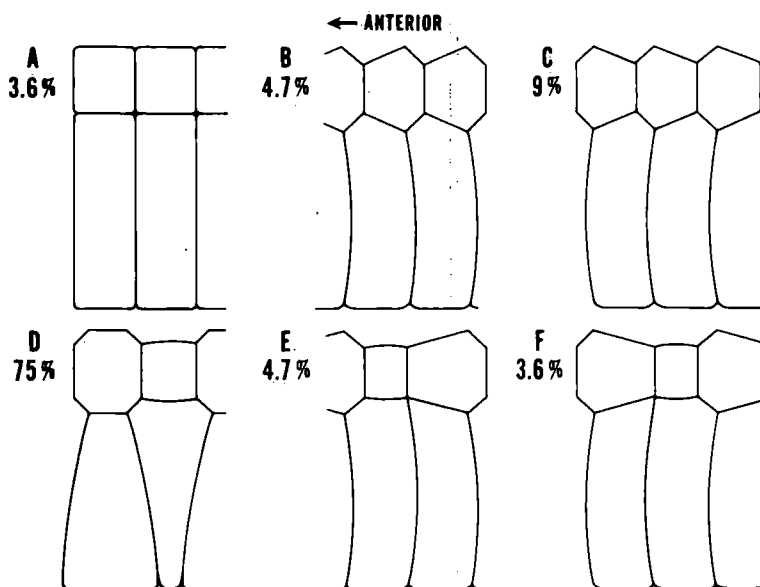


FIGURE 22.—Distribution of proximal pleural growth patterns (A-F) in *Gopherus* (all species combined) when each pleural-neural pair is considered as a single independent unit.

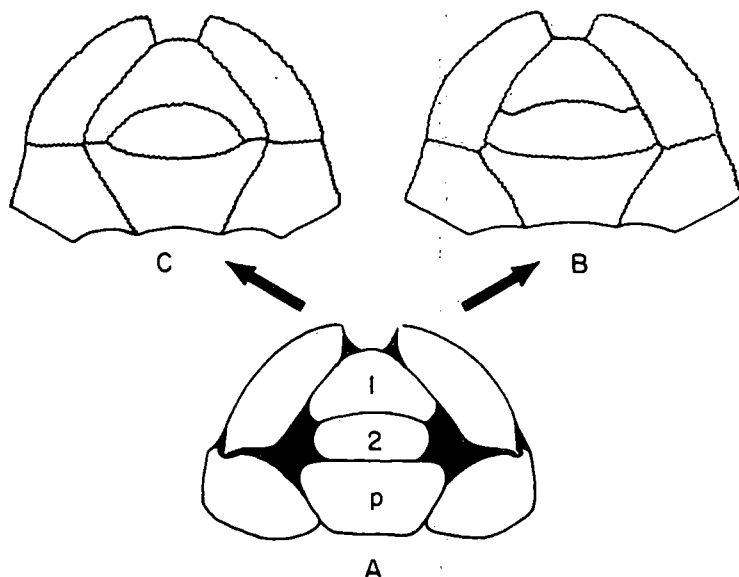


FIGURE 23.—Ossification patterns in pygal area of *Gopherus*. A, hatchling condition with fenestra shown in black. B and C, derived adult bone patterns, depending on whether supra-pygals 1 or 2 fill the fenestra. p=pygal bone.

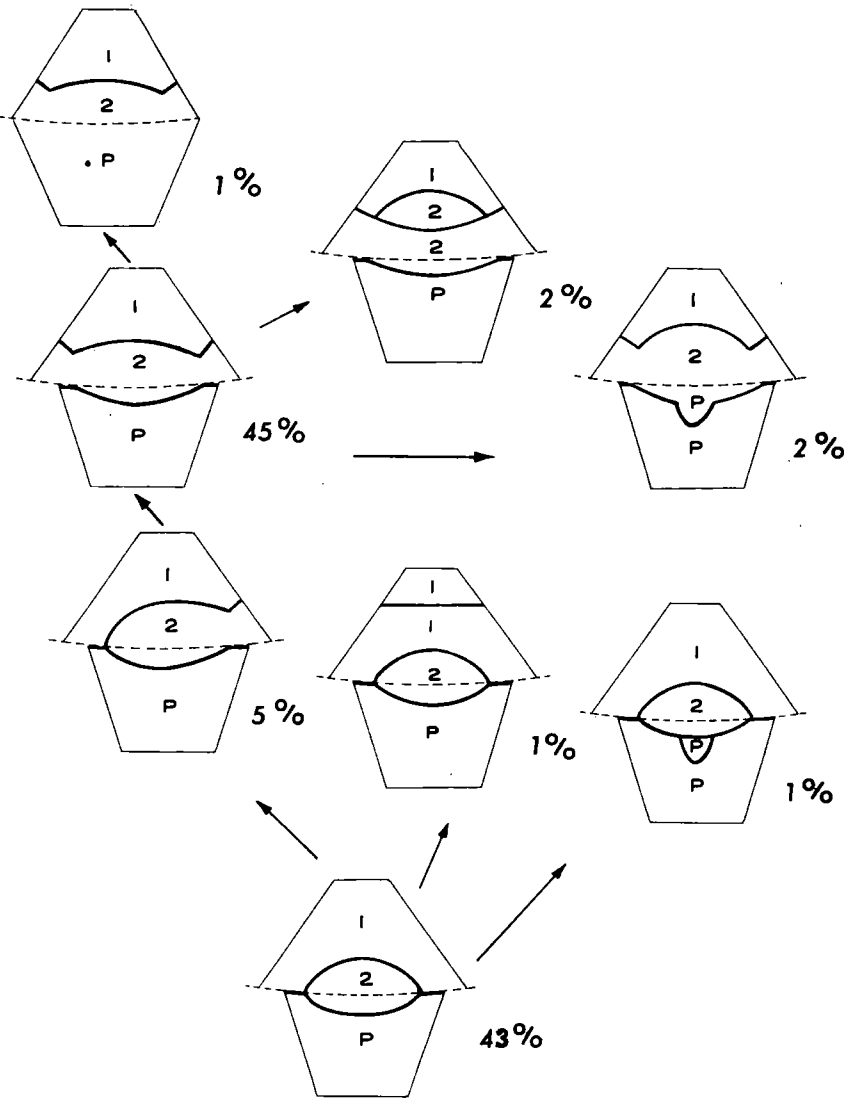


FIGURE 24.—Variation in ossification patterns of *Gopherus* (all species combined).
1 and 2=suprapygals 1 and 2, p=pygal.

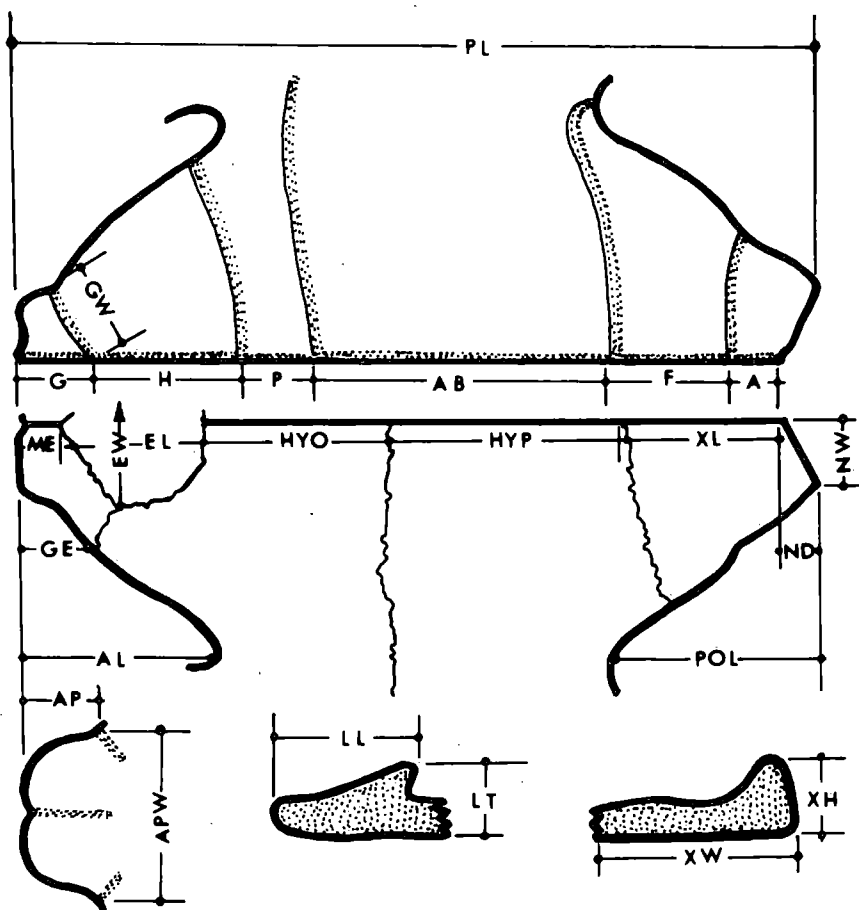


FIGURE 25.—Plastral measurements used in this study. Stippled drawings are cross sections of plastral lip (left) and xiphiplastron (right). Abbreviations: A, anal; AB, abdominal; AL, anterior lobe length; AP, anterior projection length; APW, anterior projection width; EL, entoplastron length; EW, entoplastron width; F, femoral; G, gular scute length; GE, greatest epiplastron length; GW, gulo-humeral sulcus; H, humeral; HYO, hyoplastron; HYP, hypoplastron; LL, epiplastron lip length; LT, lip thickness; ME, median epiplastral length; ND, anal notch depth; NW, anal notch width; P, pectoral; PL, plastron length; POL, posterior lobe length; XH, xiphiplastron height of outer surface; XL, xiphiplastron length; XW, xiphiplastron width.

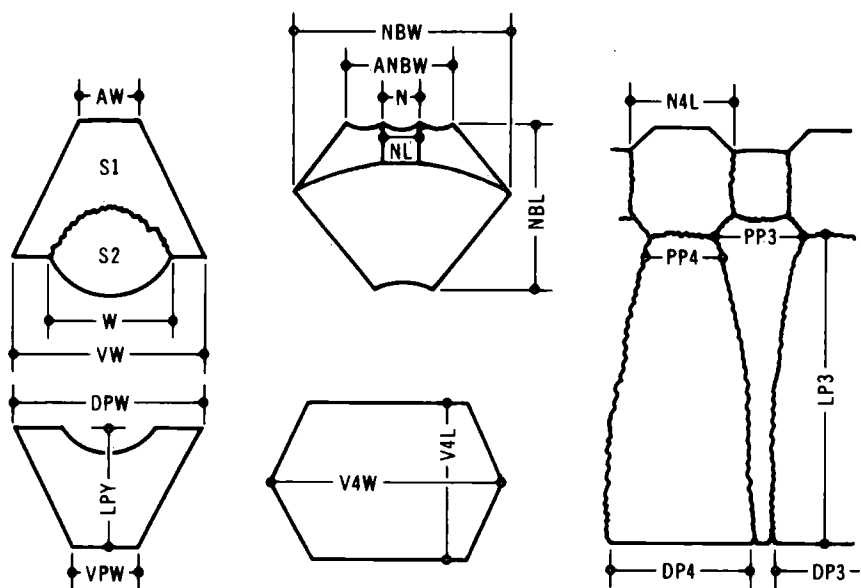


FIGURE 26.—Carapace measurements used in this study. Upper left, suprapygals 1 and 2. Lower left, pygal. Upper middle, nuchal bone. Lower middle, 4th vertebral scute. Right, neural and pleural bones. Abbreviations: ANBW, anterior nuchal bone width; AW, dorsal width suprapygal 1; CL, carapace length; CW, carapace width; CH, carapace height at highest point; DP₃, distal width pleural 4; DPW, dorsal width of pygal bone; LP3, length pleural 3; LPY, length pygal bone; NBL, nuchal bone length; NBW, nuchal bone width; NL, nuchal scute length; NW, width nuchal scute; N4L, neural 4 length; PP₃, proximal width pleural 3; PP₄, proximal width pleural 4; S1L and S2L, suprapygals 1 and 2 lengths; S1W and S2W, suprapygals 2 and 3 widths; V2W, vertebral scute 2 width; V2L, vertebral scute 2 length; V4W, vertebral scute 4 width; V4L, vertebral scute 4 length; VPW, ventral pygal bone width; VW, ventral width suprapygals 1.

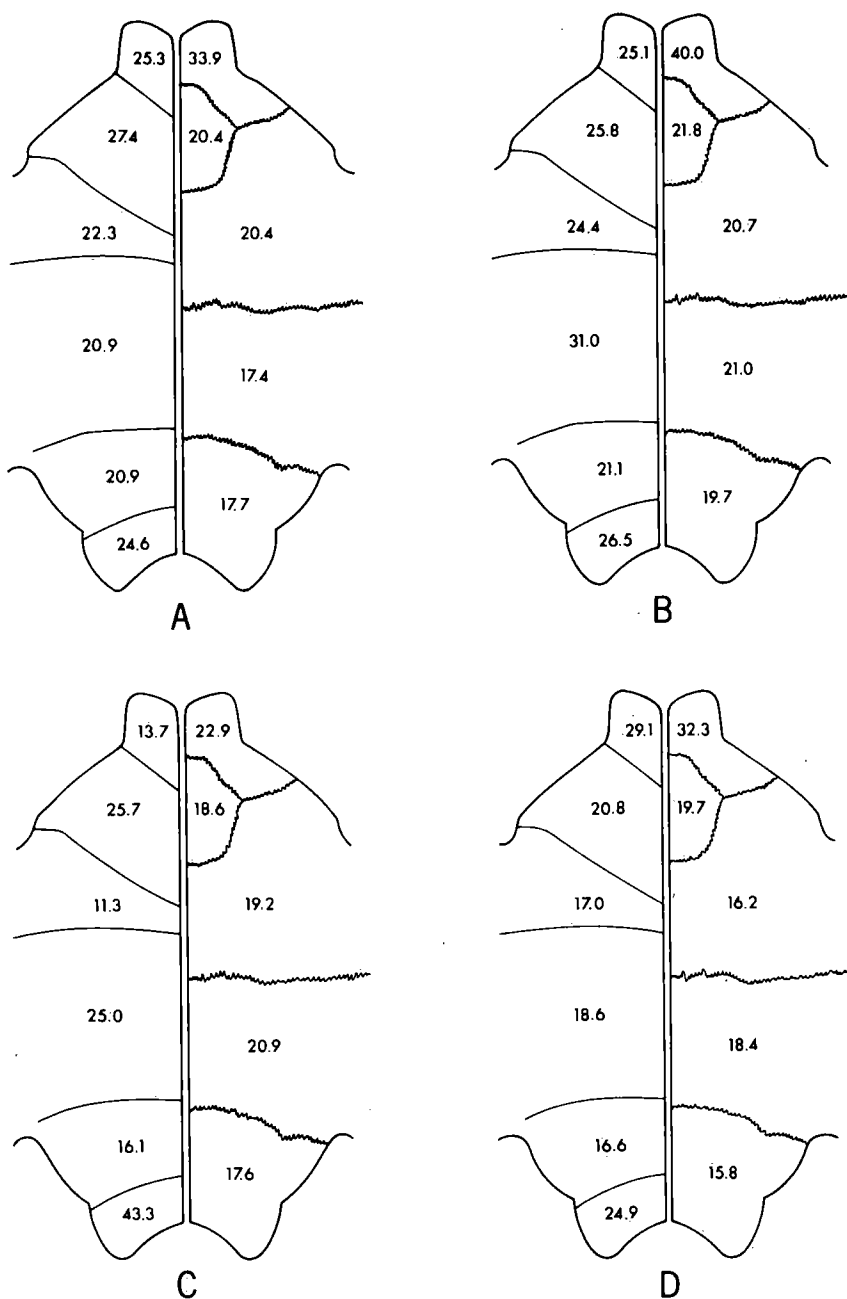


FIGURE 27.—Comparison of coefficients of variation in median lengths of plastral scutes (right) and bones (left) in the extant species of *Gopherus*. A) *agassizi*; B) *berlandieri*; C) *flavomarginatus*; D) *polyphemus*.

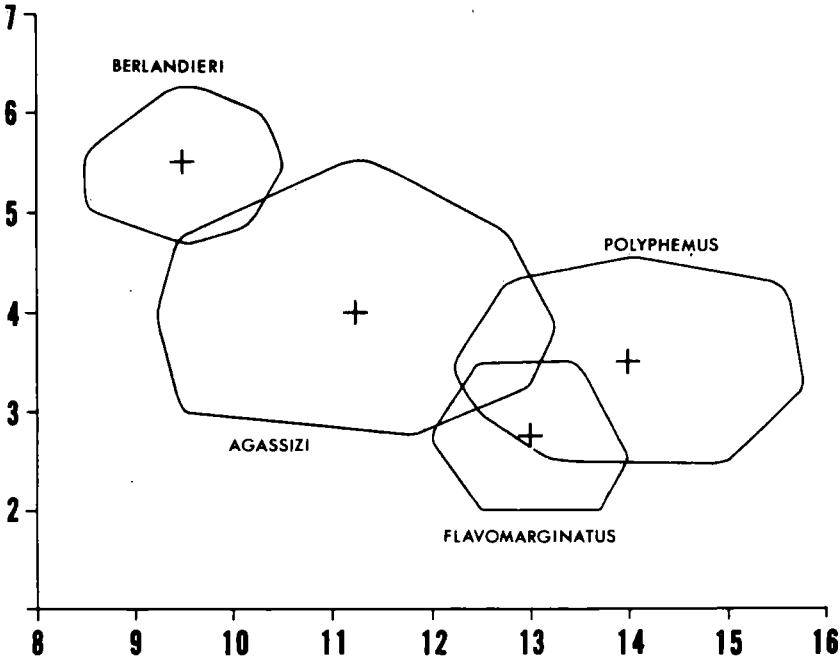


FIGURE 28.—Linear discrimination of *Gopherus* species. The contours indicate the extreme range of individuals in the populations used. The *berlandieri-polyphemus* discriminant function is used as the ordinate, the *berlandieri-agassizi* discriminant function as the abscissa.

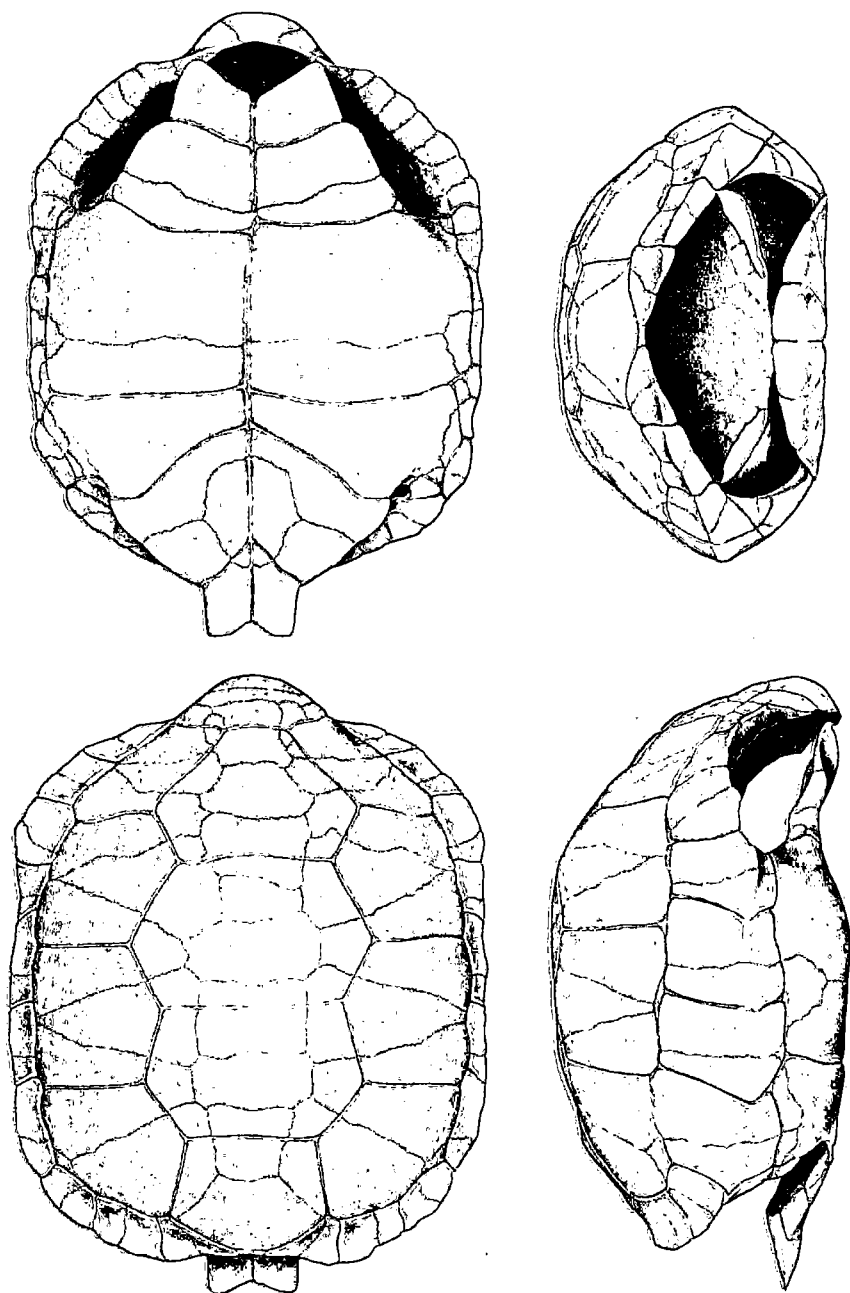


FIGURE 29.—Shell of adult *Gopherus berlandieri*.

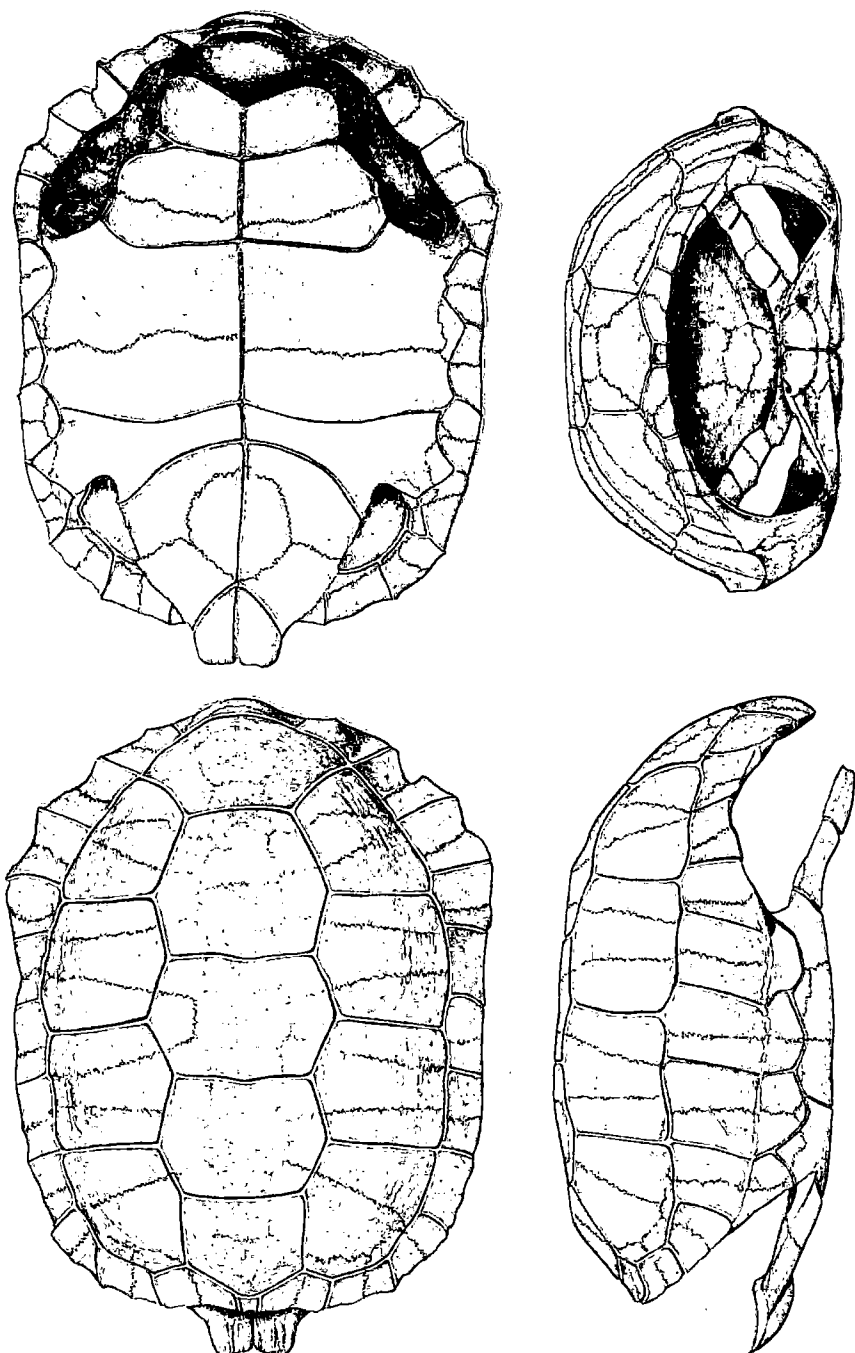


FIGURE 30.—Shell of adult *Gopherus agassizi*.

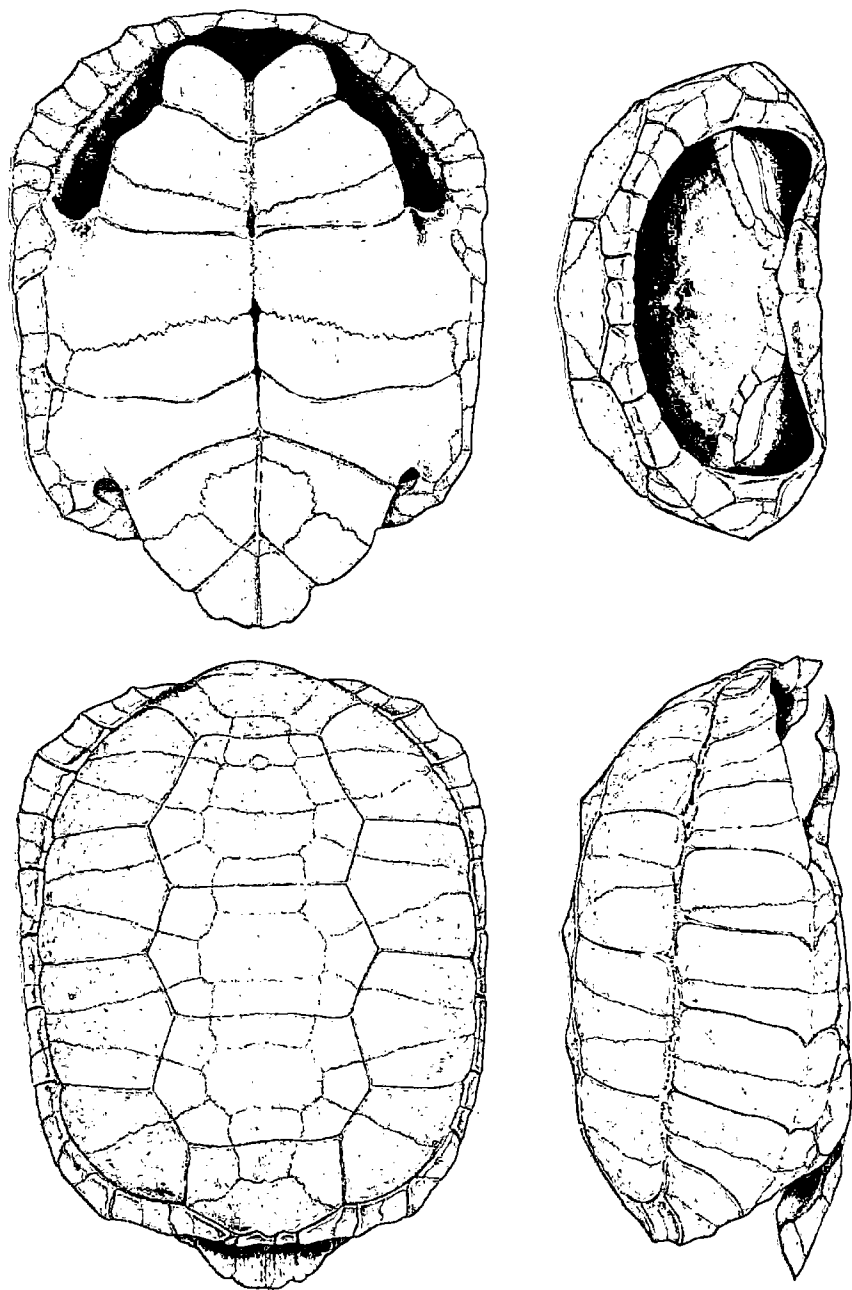


FIGURE 31.—Shell of adult *Gopherus flavomarginatus*.

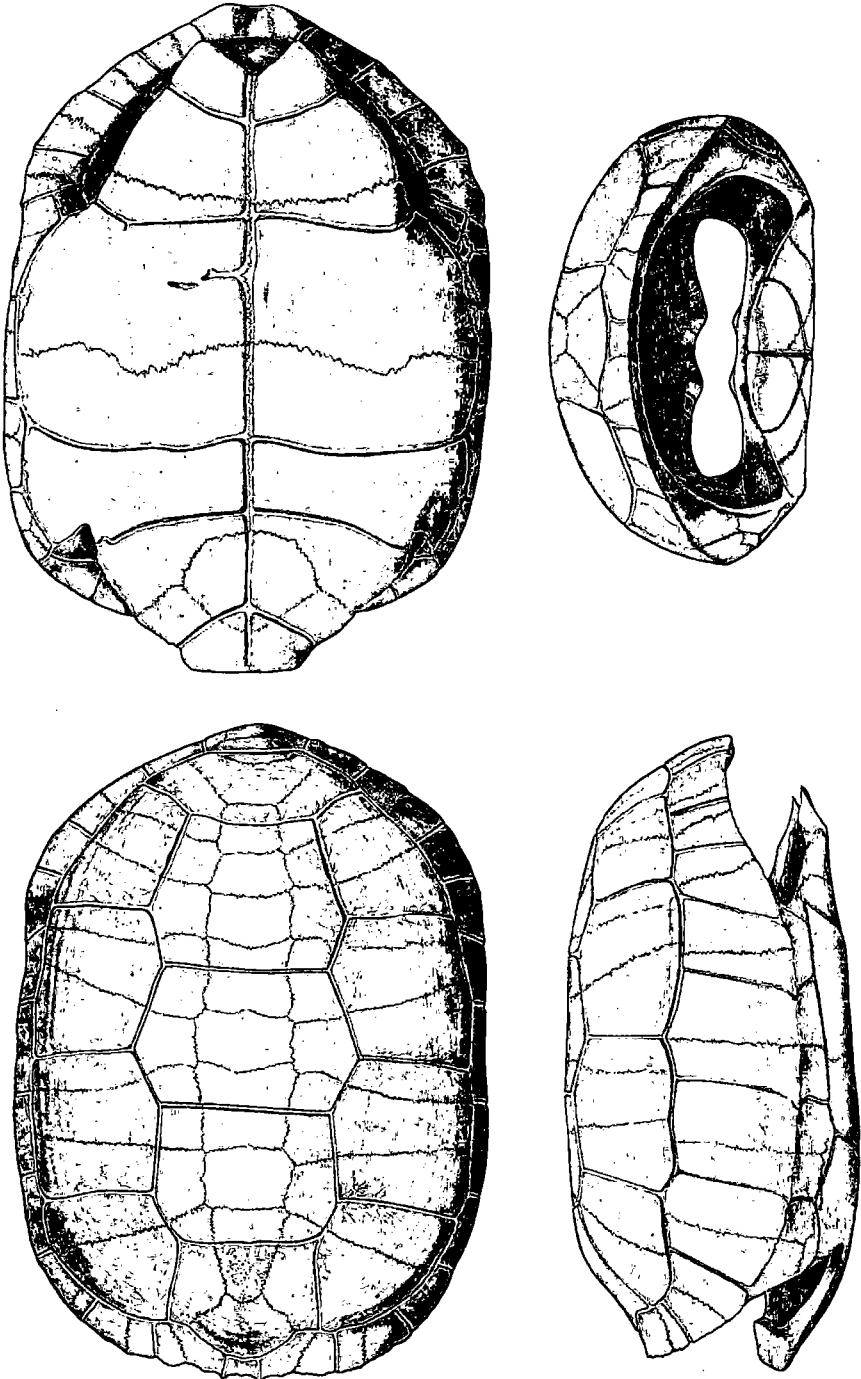


FIGURE 32.—Shell of adult *Gopherus polyphemus*.
































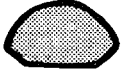




	BERLANDIERI	AGASSIZI	FLAVOMARGINATUS	POLYPHEMUS
I PYGAL SHAPE	 5.65	 2.39	 5.22	 1.78
II BRIDGE MARGINALS (X-SECTION)				
III SHELL FLAIR OVER HIND LEGS				
IV SHELL POSTERIOR FROM ABOVE				
V SHELL X-SECTION	HIGH	MOD- SLIGHTLY DEPRESSED	SLIGHTLY DEPRESSED	DEPRESSED
VI HIGHEST POINT ON SHELL	BEHIND MIDDLE	USUALLY AT MIDDLE	MIDDLE OR ANT. TO MID.	MIDDLE OR ANT. TO M.D.
VII WIDEST POINT ON SHELL	BEHIND MIDDLE	BEHIND MID., BUT LESS MARKED	MIDDLE TO BEHIND MID.	USUALLY AT MID. SIDES OFTEN PARALLEL
VIII EPIPLASTRAL LIP X-SECTION				
IX PLASTRON				
X ENTOPLASTRON				
XI PERIPHERO- PLEURAL ARTICULATION	FIRMLY FUSED	GENERALLY FIRMLY FUSED	OFTEN FENESTRAL	SMALL FENESTRA COMMON
XII TRANS-X-SEC. SHELL				
XIII EPIPLASTRAL PROJECTION (♂)				

FIGURE 33.—Qualitative shell differences in the extant *Gopherus* species. Numbers adjacent to each of the pygals are the average values for anterior/posterior widths.

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