

THE GILA MONSTER
AND ITS ALLIES

THE RELATIONSHIPS, HABITS,
AND BEHAVIOR OF THE
LIZARDS OF THE
FAMILY HELODERMATIDAE

CHARLES M. BOGERT
AND
RAFAEL MARTÍN DEL CAMPO

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INTRODUCTION

THERE HAVE BEEN numerous contributions to our knowledge of the beaded lizards, or Gila monsters, but no one appears to have examined more than a few specimens at any one time. The distributions and the relationships of the two species comprising the single genus in the family have remained poorly understood.

Our study of the beaded lizards began independently when each of us obtained specimens of *Heloderma horridum* from the Atlantic drainage of Chiapas, where the species had not previously been recorded. The first specimen was obtained for the American Museum of Natural History by Thomas MacDougall in 1945, while he was carrying out botanical explorations in the region. Later both of us received additional material through the courtesy of Señor Miguel Alvarez del Toro, who maintains a small zoological garden at Tuxtla Gutiérrez in Chiapas. The specimens were so obviously different in coloration from those from the Pacific slope that each of us decided to make more detailed comparisons. However, during the summer of 1950 we met in México City, and after discussing the problems involved we decided to publish a joint paper.

After the literature had been examined and material for the study had been assembled, it became manifest that the study could profitably be extended. We have, therefore, attempted to summarize the information already in print, and to present the results of our study of the material so generously placed at our disposal by numerous individuals and institutions.

Supplementing our taxonomic conclusions, we present a review of what is known concerning life histories, the behavior, and the ecology of the lizards of the family, together with a summary of information concerning the venom, venom apparatus, and the effects of envenomation.

The taxonomic conclusions we have drawn are based on a survey of the literature and an examination of alcoholic specimens and skeletal material. Of *H. horridum* we have seen 54 alcoholic specimens, two complete skeletons, all but the caudal vertebrae of a third, and four additional skulls. We have also had available over 120 specimens of *H. suspectum* either alive or preserved, in addition to eight complete skeletons, a small specimen cleared and stained, and three skulls. Through the kindness of Dr. E. H. Colbert of the American Museum we have examined the only described fossil from North America correctly assigned to the family Helodermatidae.

Mr. Arthur Loveridge of the Museum of Comparative Zoölogy at Harvard College generously allowed us to remove the skull of the only specimen of *Lanthanotus* known to be represented in any museum in the United States. As a result we have been able to compare the skull of *Heloderma* with that of the Bornean lizard, and to make additional comparisons that are more nearly adequate than any previously reported. Detailed comparisons of *Lanthanotus*, *Heloderma*, and related genera have been published elsewhere (see McDowell and Bogert, 1954).

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specimen of *H. suspectum* in the Philadelphia Zoological Garden, to Mr. Weldon Woodson for assistance in locating specimens from critical areas within the range of *H. suspectum*, as well as for locality records, and to Dr. Charles H. Lowe of the University of Arizona, who was extremely helpful in providing specimens. We are grateful to Mr. and Mrs. George M. Bradt of Tucson, Arizona, for specimens and photographs, as well as for hospitality. Mr. Alden Hayes of Portal, Arizona, and Dr. William Koster of the University of New Mexico also supplied data.

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ORIGINAL DESCRIPTIONS AND TYPE LOCALITIES

As far as known, the earliest description of a helodermatid is that of Hernández who in 1615 (Latin edition, abstracted by Nardo Antonio N. Reccho, first published in 1628, with a second edition in 1651, according to Klauber, 1948) described the "*Acaltetepon*," mentioning the fact that it is found on the fields of Cuernavaca ("*Versatus in Quauhnahuacensibus agris*") in the present state of Morelos. On page 58, in an appendix to the first Latin edition (we have seen only the second), Hernández discusses venomous animals in Nova Hispania and mentions a second "*Acaltetepon*,"

which to judge by the description probably refers to an animal that is not closely related to the lizard now known as *Heloderma horridum*. However, Wiegmann in 1834 assumed that it was related, and proposed the name "*Heloderma Hernandezii*," which has sometimes been cited in the synonymy of *H. horridum*.

In a paper on the geographic distribution of lizards published in 1829, Wiegmann (in a footnote, p. 421) was the first to use a binomial, applying the name *Trachyderma horridum* to a specimen collected by Ferdinand Deppe in

"Mexico." He describes the grooved teeth and wonders how venom could be directed upward from those in the lower jaw. He notes that the animal is the same as that referred to by Hernández as the Acaltepon. On page 627 of the same volume Wiegmann notes that *Trachyderma* is preoccupied. Consequently he proposes the name *Heloderma* for the genus, which he describes along with the species, *horridum*. Wiegmann notes on page 421 that a "*schöne Abbildung*" will appear in Wagler's forthcoming work, which was published the following year, 1830 (1830a).

Wagler depicts a stuffed specimen in a colored plate that supposedly represents the same specimen Deppe supplied to Wiegmann. The lizard is shown as being black, with a few yellow scales on the limbs, neck, and trunk, and with five yellow bands, one of them interrupted by a row of black scales, on the tail. Wagler also supplies a description, including measurements that are not identical with those given the previous year by Wiegmann. Possibly the original measurements were of the skin, not measured by Wagler until it had been mounted. Schinz and Brodtmann (1833) depict the same specimen.

Apparently the "*schöne Abbildung*" was not all that Wiegmann had hoped for, because in 1834 he notes the inaccuracies in Wagler's plate, and offers one of his own [badly copied by Duméril, Bibron, and Duméril, 1836 (1834-1854)] accompanied by his earlier (1829) description. His figure, depicting the left side rather than the right already illustrated by Wagler, shows a reptile with a proportionately smaller head, thinner limbs, and considerably more indication of a pattern comprised of brownish areas within a black reticulum, and having more individual scales emphasized in yellow than Wagler indicated. There are numerous other minor discrepancies in the two drawings, despite the fact that they represent the same specimen. Whereas the respective plates leave no doubt concerning the identity of the species, their identity with any of the local populations now represented in collections is problematical. It may be assumed that the lighter areas in the pattern had become darkened prior to the arrival of the skin in Europe. However, a specimen from Chilpancingo, Guerrero, in the collection of the Chicago Natural History

Museum is as dark as or darker than the animal shown in Wiegmann's plate.

The Gila monster, *Heloderma suspectum*, the only other surviving species of the genus, first became known to science in 1859 when Baird listed or described many of the reptiles collected by members of the Mexican Boundary Survey under the command of Lieutenant Colonel W. H. Emory. Using the name *Heloderma horridum*, Baird lists the museum catalogue number, the locality and the collector: "2971. Sierra de la Unión, Sonora. A. Schott." In a moderately good plate he portrays a specimen that he presumed to be Wiegmann's species. It was not until a decade after the publication of the plate that anyone realized that the specimen depicted by Baird represented another species.

On March 9, 1869, Cope attended a meeting of the Academy of Natural Sciences of Philadelphia where he exhibited a specimen of *H. horridum*. He noted that it differed from the "*Heloderma* of the Sonoran region," stating that the latter had more numerous scales on the head and body, as well as a shorter tail and different coloration. He also mentioned that the Sonoran species "had been well figured by Baird in the Mexican Boundary Survey." This information is reported in the Proceedings of the Academy, with the statement that "He [Cope] called it *H. suspectum*."

This has been universally recognized as the original description of the Gila monster. However, on the basis of Cope's remarks some authors, Van Denburgh (1922), for example, have cited the type locality as the "Sonoran Region," whereas Stejneger and Barbour (1917, and in later editions of the "Check list") and others, having referred to Baird's paper, give it as "Sierra de la Unión, Arizona ('Sonora')." Actually the north end of the small mountain range called Sierra de la Unión is approximately 8 kilometers south of the International Boundary on modern maps. Smith and Taylor (1950b) cite the type locality as "Sierra de la Unión, 'Sonora' (=Arizona)," mentioning "three co-types" under the U.S.N.M. No. 2971. Earlier the same year (1950a) they had listed the locality more nearly correctly as "Sierra de Morena (=Sierra de la Unión, 10 miles southwest of San Miguel)" in Pima County, Arizona. As the Arizona town

of San Miguel is approximately 6 miles northeast of the Boundary, the mileage indicated, if taken literally, would place the type locality in Sonora.

Fortunately the report (Barlow, Gaillard, and Mosman, 1898) of the Boundary Commission under Colonel J. W. Barlow states that monument "No. 146 . . . marks the highest point where the boundary crosses the Moreno Mountains, the 'Cerro de la Union' of the Emory Survey," of which Schott was a member. The 1:500,000 map included in the "Atlas geográfico," published in México and dated 1943, shows individual monuments by number, with No. 146 falling on the hill labeled Sierra de Moreno. Hence the type locality of *H. suspectum*, at least in theory, falls directly on the International Boundary, at Monument 146, or Sierra de Moreno.

Somewhat similar problems have been posed concerning the type locality of *H. horridum*. Originally given as "Mexico" by Wiegmann, it was restricted by Smith and Taylor (1950a) to "Hua jintlán (at Morelos border)" in the state of Guerrero. Actually the town by this name is in the state of Morelos, although Smith (*in litt.*) informs us that the specimen originally reported (H. M. Smith, 1935) as taken "eleven miles southwest of Puente de Ixtla [in Morelos], Guerrero," is the same one later catalogued as being from Hua jintlán. Having been taken a few hundred feet west of the edge of the town, it is actually from the state of Guerrero.

In view of the fact that Hernández states, "*Versatur in Quauhnahuacensibus agris . . .*" ("*Cuauhnahuac*" being the Indian name, meaning "in front of the forest," for the capital city of Morelos, now known as Cuernavaca) and is so quoted by Wiegmann (1834), it would seem more appropriate to designate Cuernavaca, Morelos, as the type locality. The type specimen did not necessarily come from Morelos, but the specimen from Cañón del Lobo near Cuernavaca in the Museo Nacional de Historia Natural in México City proves that the species occurs as far inland as Cuernavaca. However, the record is peripheral as far as present knowledge indicates. The type specimen of *H. horridum* probably came from some locality not distant from México City. In any event the exact source of the type is more or

less academic.

Although fossils of several extinct lizards have been referred to the Helodermatidae, Gilmore (1928) has indicated that all of them until the date of his publication have their affinities elsewhere. The only fossil¹ assigned with certainty is a portion of the left maxilla containing three grooved teeth. These are astonishingly similar to those of the existing species, with minor differences pointed out by Gilmore, who described the type specimen and assigned the name *Heloderma matthewi*. The fossil was found in an Oligocene deposit, the Oreodon zone of the White River formation in Logan County, Colorado. The type locality is east of the Rocky Mountains, considerably beyond the present range of *suspectum*, which is restricted to the Pacific drainage, and unknown north of extreme southwestern Utah, or east of southwestern New Mexico.

¹ After the present report had been submitted for publication, Robert Hoffstetter sent us a reprint of his paper (1954) describing a fossil helodermatid from the Phosphorites of Quercy (Eocene-Oligocene). With four maxilla almost complete, a dentary without teeth, a pterygoid, and some vertebrae, Hoffstetter observes that they represent an animal of greater size than *Heloderma suspectum*, although morphologically they are virtually identical. The osteoderms are firmly ankylosed to the maxilla but are larger and fewer in number than in living species. From nine to 11 maxillary teeth are feebly pleurodont and inserted obliquely, with dilated bases. Cutting edges are present on the teeth, with a feeble groove along the anterior edge. Seven small pterygoid teeth are present. The similarity of the bones to those of existing species, as well as to the fragment on which *H. matthewi* was based, is sufficiently close that Hoffstetter believes there is no doubt concerning the affinities of the fossil, which should be referred to *Heloderma* or a closely related genus.

Without additional material from North America it cannot be ascertained whether the European fossil differs appreciably from *H. matthewi* of similar age. However, it is noteworthy that more maxillary teeth are present in the fossil than in either species of *Heloderma* now living. However, the pterygoid teeth are not more numerous, as Hoffstetter states, because as many as seven can be detected in some specimens of *H. horridum*. While the grooves in the teeth of *H. matthewi* are comparable to those of *H. suspectum*, the feeble grooves in the European fossil point to a less specialized venom apparatus, as Hoffstetter notes, pointing out that this is the first indisputable helodermatid to be found outside North America. Its discovery shows that helodermatids inhabited western Europe during the upper Eocene or the lower Oligocene, quite probably at the same time that *H. matthewi* was roaming the region now in Logan County, Colorado.

Haury (1950) lists the vertebrate remains, most of them recent or sub-recent, taken in Ventana Cave, Pima County, Arizona, and through a *lapsus calami* the name of the Gila monster is given as "*Heloderma maculatum*." There was no intention of applying a new name to the bones found in the cave, which is within the known range of *H. suspectum*.

Hobart M. Smith (1949) comments on the

name *Heloderma europaeum* Nicolussi, 1934, "proposed for an animal of which the only evidence was a photograph, which itself may have been a hoax." Smith adds that "such names for mythical species can be considered unoccupied . . . they are unscientific." The two living species have not been confused with other reptiles, and no names other than those mentioned above have ever been applied.

DISCUSSION OF CHARACTERS

Except for Gadow's (1901) pointless comment that "the specific differences [between the two species of *Heloderma*] are rather imaginary," no one has ever seriously questioned the status of the species. The "shorter tail" of *suspectum* referred to by Cope (1869) at the time he proposed the name readily serves to distinguish individuals of the species from those of *horridum*, provided, of course, that the tail length is expressed as a ratio. Aside from the proportionally shorter tail of *suspectum* and the characters of scutellation and pattern associated with it, there are other morphological differences that point to the specific distinctness of the two; as far as can now be demonstrated their ranges are allopatric. Despite many similarities in morphology and behavior, it seems doubtful whether they would interbreed even were their ranges to overlap.

There has been no need, therefore, to demonstrate that the genus is represented by two living species. However, we have attempted to ascertain the extent of the variation within each species. Primarily this was done in order to gain a better understanding of the clines or geographical trends demonstrable in the samples available. To this end we have tabulated data for approximately 30 characters of the scutellation and the proportional dimensions. In addition we have made use of pattern characters, few of which can readily be described in quantitative terms. The skeleton is doubtless subject to more variation than the limited data at our disposal would indicate. Our examination of osteological characters has brought to light differences between the species hitherto unrecorded. However, we have not attempted to compare skeletal characters at the subspecific level.

Both species of *Heloderma* have been de-

picted numerous times, but no one has ever attempted to describe many of the variations. Indeed it has only been within the last decade that specimens of *horridum* from Sonora and Chiapas have been available. Characters that Cope (1900) termed "constant" are subject to considerable variation, whereas others not mentioned by him prove to be of value in segregating species as well as subspecies. To clarify the descriptions and diagnoses in the following sections the names of individual scales or series of scales referred to in the text have been indicated in plate 2. The space limitations in the plate have necessitated that only one or two scales in some series be designated, or, in some instances, merely the general region (of the gular scales, for example).

Plate 2 supplies sufficient information to enable the reader to identify most of the scales on the head. But some scales or scale series are too variable to be depicted accurately. The rostral is not always so well defined as it appears in the plate, particularly in the races of *suspectum*, where it is split into three scales by two vertical sutures in approximately 10 per cent of the specimens. This is the condition shown in Cope's figure reproduced as our text figure 9. The lateral portions of the rostral are not readily distinguished from the first supralabial, unless the latter is defined as the scale located below the prenasal. So that comparable counts of the supralabials could be made, therefore, the scales properly considered to be portions of the rostral have been excluded from the labial counts on this basis.

The prenasal, the supranasal, and the postnasal are always single. The supranasal may either be in contact with the postnasal or separated from it by the first canthal, as shown in plate 2. When the first canthal is excluded from

the nasal by the contact of the supranasal and the postnasal, the first canthal may be shifted somewhat towards the middle of the snout and not fall in direct line with the other scales on the canthal ridge. In some instances one or more of the posterior canthals are not situated on the ridge, so that some judgment must be exercised to decide, for example, whether a scale is to be called an upper loreal or a canthal. The lorilabials may be in a single row, in two rows, or individual scales may be wedged in between those in the normal series; all such scales have been included in the counts for lorilabials. Sometimes the anterior lorilabial separates the first supralabial from the nasal, or the latter plates may be in contact. Such conditions have been recorded and prove to be of some interest from the clinal viewpoint, even though the differences between populations in this respect are not sufficiently constant to be of taxonomic value.

Owing to the fact that the scales in some series on the head are irregularly disposed, rather than being in rows, it is sometimes difficult to make counts that can be repeated without a small margin of error. However, we find that it is possible to count the scales across the head by following a more or less straight line between the posteriormost superciliaries. On exceptional specimens the count obtained by one person may differ by one scale from that obtained by another. Counts can also be made along the main axis between the internasals and the occiput, posterior to which the large scales on the dorsum are separated by granular scales (anteriorly the scales on the head are in contact with contiguous scales). The occiput may also be located by reference to the upper end of the ear opening, which falls at the same level. Regardless of which method is used to terminate the count at the occiput, any count can be duplicated with an error of no more than one scale. Similarly the scale count between the gular fold and the anus, which should be made slightly to one side of the middle of the belly, is subject to some error, partly because of the irregularity of the scales at the level of the limb girdles.

The rows of scales between the axilla and the groin do not always coincide at the middle, more being present on one side of the body than on the other. Nevertheless counts can

usually be duplicated when checked, or they differ by only one or two scales. Repeated counts indicate that the number of scales around the middle of the body, as well as around the base of the tail, can usually be ascertained with precision; on the tail the count was made from seven to nine scales posterior to the vent, as the rows immediately behind it curve upward on the sides of the tail at an oblique angle. Counts of the number of scale rows on the under side of the tail include all those between the vent and the terminal rosette, which is included. Care was taken to include the smaller scales in a fold immediately behind the vent, even though these are somewhat irregular.

The number of broad plates or lamellae beneath the toes is easily determined, by beginning with the first undivided scale at the base and counting distally to the claw, which is of course excluded.

Despite the minor shortcomings of some of the characters in the scutellation tabulated, many of them satisfactorily serve to demonstrate trends indicative of the degree of evolutionary divergence of the populations represented.

Greater emphasis has been placed on scale characters than on those requiring computation of ratios, with the exception of that for the tail to the snout-vent length. One handicap in using ratios lies in the fact that the proportions of the lizards in the genus *Heloderma* are subject to ontogenetic changes. But the greatest difficulty lies in obtaining reliable measurements for some parts of the individual specimen. Most specimens of *Heloderma* have been preserved with the body distorted in some fashion, commonly with the tail curled forward beside the trunk. Owing to the thick skin, studded with osteoderms on portions of the limbs and on the upper surface of the body, it is virtually impossible to straighten the trunk or the limbs of many specimens that have been hardened by strong preservatives. Moreover, many specimens, particularly of the larger species, are not well preserved. Even when a slit had been cut in the abdomen, extensive fat bodies located in the abdominal cavity just anterior to the pelvic girdle had prevented penetration of the preservative. As a result the pelvic region is often so badly decomposed that the limbs and the tail could not be straightened

without further destruction of the specimen.

It has been possible to apply a meter stick to obtain the measurements from the snout to the vent of a few specimens preserved with the main axis of the belly and tail in a straight line, the tail being measured from the vent to the tip, rather than from the insertions of the hind limbs. To obtain such measurements from distorted specimens it is necessary to use a piece of soft wire (solder is excellent for the purpose), one end of which is held in place on the head at the level of the snout while the wire is applied to the body, centimeter by centimeter, care being taken to keep the wire directly above the spine. The wire, with points marked to indicate the location of the vent and the tip of the tail, is then measured with a meter stick. It is not possible to say how closely measurements obtained in this manner correspond to those that might be made of the animal in life. Whereas the method provides more reliable information than can be obtained by applying a meter stick or a tape measure to a distorted specimen, the measurements, particularly of the body, are to be considered close approximations rather than accurate measurements. The same is true of those for hind limbs obtained by distending the limbs to the fullest extent possible and measuring the distance between the base of the claw of the longest digit of each outstretched foot. The measurement could not be obtained for approximately 25 per cent of the specimens examined owing to their stiffness or their partial decomposition.

Distances between points on the head could be measured accurately with Vernier calipers. Three measurements were made: (1) the distance across the head between the posterior superciliary of each side; (2) the greatest diameter of the head, which falls at the temporal region; and (3) the head length, considered to be the distance between the upper end of the ear opening and the center of the rostral. The straight-line distance between the tip of the claw and the distal edge of the supradigital scale at its insertion was measured to obtain the claw length, such measurements having been restricted to the claw of the third or fourth digit when the point was intact.

Other features of the morphology mentioned in the descriptions that follow have been explained in the text when necessary. We attempt

to describe the ontogenetic variations and the geographical trends in pattern, but to avoid overly detailed descriptions we have relied heavily on plates depicting specimens representing the subspecies recognized.

We have discovered no external character that serves to distinguish the sexes. There are slight differences between the sexes in the means for some ratios, as well as for some scale counts, but in no instance are the differences statistically significant, much less of any practical value in determining the sex of an individual. A slit at the base of the tail will usually disclose the presence of hemipenes in males, but in some poorly preserved specimens the results of such dissections are questionable. Consequently we have relied upon an examination of the gonads. In more than 20 juveniles examined the gonads proved to be flattened ovoid structures superficially similar to the testes of adult males. In half-grown specimens, presumed to be in their second or third year, however, it was possible to distinguish between testis and ovary without difficulty. It is probable that differentiation in the gonads does not occur until sometime during or after the second year of life.

We have attempted to ascertain the sex of living specimens by using a probe, assuming that it could be thrust through the vent into the tubular hemipenis of the male, as it can in most snakes. Three specimens of *H. suspectum* were available with over-all lengths of 416, 445, and 460 mm., respectively. In the smallest the probe could be inserted to a depth of 22 mm., of the next to 15 mm., and in the largest specimen 30 mm. of the probe readily penetrated. We assumed that the middle-sized specimen was a female, whereas the other two were believed to be males. However, the method proved to be unreliable. Dissections after death disclosed that the largest of the three specimens was indeed a male, whereas our assumptions concerning the two smaller individuals were wrong.

There is, therefore, no reliable means of ascertaining the sex of beaded lizards while they are alive. Unfortunately captive specimens rarely attempt to copulate, although such behavior might provide useful clues concerning sex.

CLASSIFICATION AND DISTRIBUTION OF THE BEADED LIZARDS

FAMILY HELODERMATIDAE¹

Helodermidae GRAY, 1837, Proc. Zool. Soc. London, p. 132; 1845, Catalogue of the lizards in the . . . British Museum, pp. 3, 14. COPE, 1864, Proc. Acad. Nat. Sci. Philadelphia, vol. 16, pp. 227, 228. SMITH AND TAYLOR, 1950, Bull. U. S. Natl. Mus., no. 199, p. 192.

Helodermatidae BOULENGER, 1884, Ann. Mag. Nat. Hist., ser. 5, vol. 14, p. 120; 1885, Catalogue of the lizards in the . . . British Museum, ed. 2, vol. 2, p. 300 (part, *Lanthanotus* provisionally included). COPE, 1900, Ann. Rept. U. S. Natl. Mus., for 1898, p. 473.

DIAGNOSIS

Lizards of the family Helodermatidae are unique among the Sauria in having grooved teeth and venom glands. They are primitive platynotids believed to be somewhat remotely allied to the lizards of the family Anguinae, from which they differ in having (1) no supratemporal arch, (2) the prefrontal and postfrontal in contact above the orbit (but not always excluding the frontal from the orbital border), (3) the lateroventral processes of the paired frontals united on a suture below the olfactory lobe of the brain, (4) no parietal foramen, and (5) non-imbricating osteoderms, which are present on anterior surfaces of the limbs, and on the dorsum and sides but absent from the venter, except in the preanal region. (See fig. 1.)

Helodermatids resemble the Bornean species *Lanthanotus borneensis* (family Lanthanotidae) in having (1) a postorbital arch, (2) no supratemporal arch, with the squamosal reduced to a vestige, (3) the prefrontal and the postfrontal in contact, (4) no parietal foramen, (5) vestigial palatine and pterygoid teeth, and (6) a tongue composed of two distinct portions, a thick basal portion covered with villose papillae, and a smooth, bifid, and protrusible distal portion. However, *Lanthanotus* differs

from the helodermatids in having a more elongate skull with (1) the nasal bones coalesced to form a single bone, (2) the supraoccipital united with the parietal, (3) the vomers broadened and united throughout their length, (4) the splenial separated from the surangular by the suture of the articular and the coronoid, (5) three vertebrae with sternal ribs, (6) only one lumbar vertebra, (7) phalanges in both manus and pes numbering 2-3-4-4-3, (8) osteoderms restricted to a few rows of scales on the head, and (9) "pits" (probably tactile organs, absent in *Heloderma*) present on the larger scales.

The Helodermatidae have features in common with the Varanidae, notably the sutured lateroventral processes of the frontal below the olfactory lobe of the brain, the maxilla excluded from the intra-orbital vacuity (contrary to Boulenger, 1885), the scales on the back surrounded by rings of granules, the osteoderms (in some but not all varanids), four vertebrae with sternal ribs, and the phalangeal formula 2-3-4-5-3. The Varanidae differ, however, in having the postorbital arch incomplete, the temporal arch present, the nasals coalesced, and in having a parietal foramen, scale pits, and a long, slender tongue that lacks the villose basal portion.

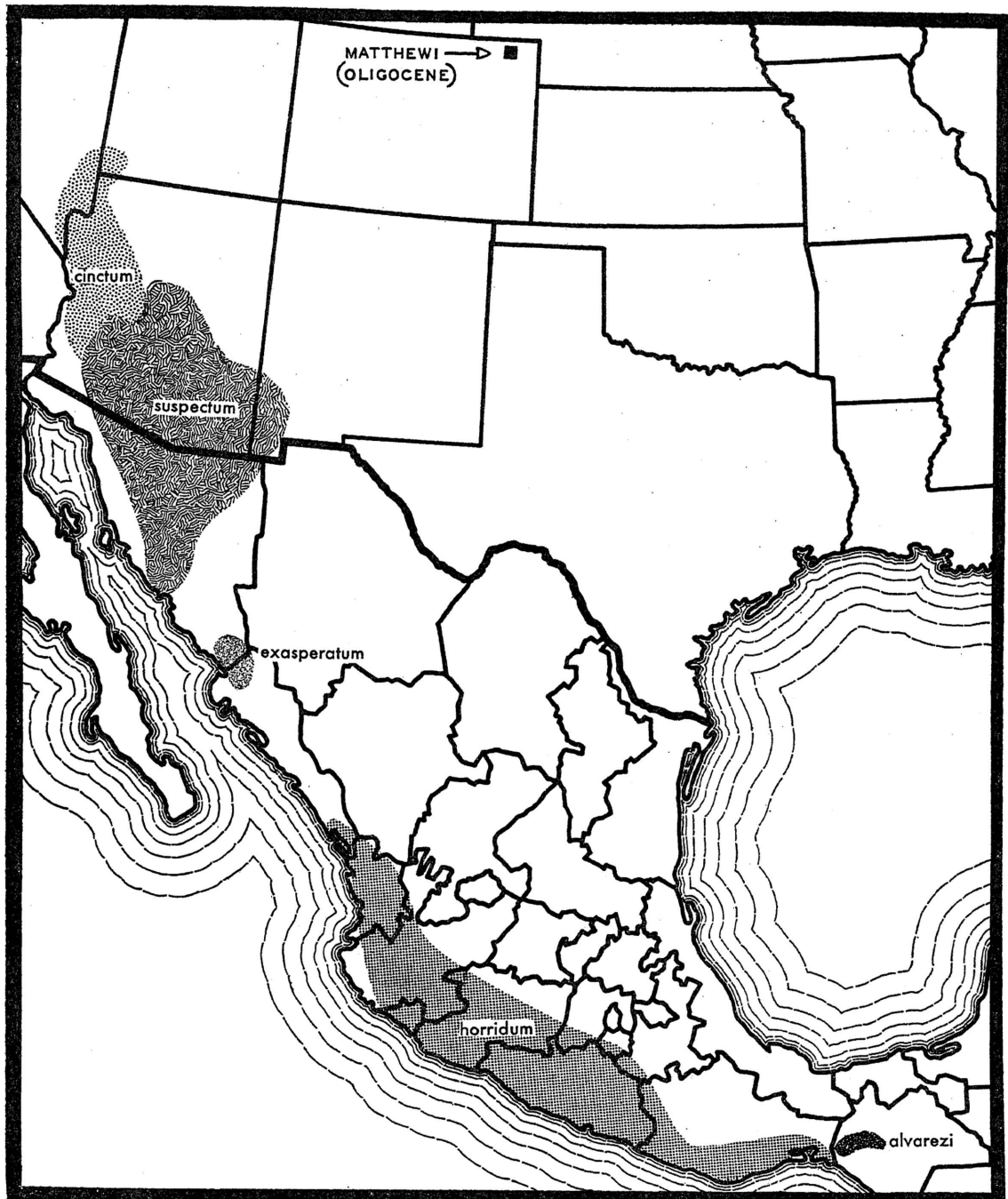
The relationships of the Helodermatidae and the Xenosauridae are not close. Barrows and Smith (1947) have pointed out numerous differences. The family Xenosauridae is evidently more closely related to the Anguinae than either family is to the Helodermatidae (see McDowell and Bogert, 1954). Information concerning the chromosomes of *Heloderma* and other lizards is supplied by Matthey (1949) and Makino (1951), but the data provided are of little assistance in working out relationships.

DEFINITION

The dentition is subpleurodont, with alternate replacement of the teeth.² The teeth of

¹ The correct spelling of the family name, with the -idae ending added to the stem rather than to the root as originally proposed by Gray. Phisalix (1922) presents a brief history of the literature dealing with the supposed relationships of the family, the affinities of which have been most recently studied by McDowell and Bogert (1954).

² The teeth, however, are not replaced in quite the simple fashion observed in snakes. For details, consult the section dealing with tooth replacement (p. 97).



MAP 1. México and contiguous portions of the United States, showing known distributions of fossil and recent lizards of the genus *Heloderma*.

the maxilla (from seven to nine) and dentary (from eight to 10) are strongly grooved at the front, feebly grooved at the back; those on the premaxilla (from six to 11) are smaller, with

the grooves much less pronounced, and usually deeper on the inner sides. As many as eight (?) teeth are present on the pterygoid, or it may be edentulous. Sometimes there are no teeth

on the palatine, or as many as five may be present. The teeth on the palatine and pterygoid are always small and neither grooved nor replaced.

The premaxilla is single; the nasals are paired; the frontals are paired and widely separated from the nasal fenestra by the dorsal process of the maxilla; the lateroventral processes of the frontals meet on an interlocking suture below the olfactory lobe of the brain. The prefrontals and postfrontals are in contact above the orbital border, usually (but not always) with a small process of the frontal entering the orbit. There is a strong postorbital arch, but the temporal arch is absent, the squamosal being reduced to a vestige attached to the supratemporal and the quadrate. The parietal is single, without a foramen. The vomers are narrow and widely separated posteriorly; the palatines are separated, as are the pterygoids. The infra-orbital vacuity is bounded by the palatine, pterygoid, and ectopterygoid, the maxilla being excluded. There is an interorbital septum.

The clavicle is slender and without a transverse process; the interclavicle consists of a longitudinal splint. The coracoid lacks emargination. The vertebral centra taper and are rounded transversely, the articular ball being set off by a distinct annular groove; there is no zygosphenes, and the neural spines are moderately high, tapering dorsally. (Pl. 1.)

The osteoderms are nodular, pitted or slightly tuberculate, non-imbricate, and fused to the bones on the top of the skull in adults. The ventral scutes are squarish, arranged in transverse series, and flattened, in contrast to the tuberculate scales of the dorsum. Scale pits as well as femoral or preanal pores are lacking. The pupil is round, with movable lids that are thick and well developed. The tongue is protrusible, with a villose basal portion, the villi being progressively shorter towards the distal end, which is smooth and bifid. The ear is exposed. The limbs are short but strong, of similar dimensions, and with the same number of phalanges both front and rear; the phalanges number 2-3-4-5-3. The digits, without exception, are clawed, with transverse shields below.

DISTRIBUTION

Lizards of the family Helodermatidae are

restricted to North America. They are known to occur as early as the Oligocene, at which time the grooved teeth were approximately as well developed as at present. Extinct forms, including *Helodermoides* described by Douglass (1903-1904) from the Oligocene of Montana, and *Placosaurus* of the upper Eocene of France, believed by Boulenger (1918) to represent a helodermatid, have all been referred to the Anguillidae by paleontologists (Gilmore, 1928).

Helodermatids are currently restricted to the Colorado River drainage of the United States, and to the Pacific slope of México, except for a small population on the Atlantic drainage of Chiapas at the Isthmus of Tehuantepec (see maps 1 and 2). Despite the moderately extensive range between the latitudes of 16° N. at the south to slightly north of 37° N., the distribution is essentially that of a relict group. Helodermatids may once have been more widely distributed, but, if we may judge by the fossil record, it seems doubtful that the family ever occupied any extensive portion of the globe. Like other surviving saurian genera, *Heloderma* once ranged farther to the north than it does at present. The fossil *H. matthewi* from Logan County, Colorado, proves that the genus at one time was represented in the area now east of the Rocky Mountain divide.

GENUS *HELODERMA* WIEGMANN

Trachyderma WIEGMANN (not of Latreille), 1829, Isis von Oken, vol. 22, p. 421; type species, *horridum*.

Heloderma WIEGMANN, 1829, Isis von Oken, vol. 22, p. 624 (substitute name for *Trachyderma*, preoccupied); type species, *Trachyderma horridum* Wiegmann.

DIAGNOSIS

The characters that serve to distinguish the family are also diagnostic of the genus.

Except for a few details in the scutellation, proportions, and pattern, the surviving species and subspecies of *Heloderma* are similar in many respects. In order to avoid repetition in the descriptions of the samples representing the species and subspecies, a general description applicable to the living representatives of the genus (the one extinct species being known only from a portion of the maxilla containing three teeth) is given here. The extremes in variation are included, but the taxonomic sig-

nificance of some of the variations is not indicated, the differences between the species and subspecies being reserved for discussion in subsequent sections of this paper.

MORPHOLOGY

The head is massive, flattened above, and broadest at the temporal region, where the width is twice the depth of the snout at the level of the loreal. The snout is bluntly rounded in outline as seen from above, and blunt in profile, with the lower jaw extending to approximately the same plane as the upper. The lower lips bulge beyond the upper, particularly below the eye. The neck is short, the distance from the occiput to the middle level of the limb insertion approximately equaling the distance from the snout to the occiput. The body is somewhat broader than the head and only slightly flattened at the venter in cross section. It tapers at the limb insertions, being somewhat broader at the pectoral girdle than at the pelvic. The distance between limb insertions of adults is approximately four times the head length, although in juveniles the head is proportionately larger. The tail is round in cross section and tapers to a blunt point, often a rosette of scales, never a single spine. The tail comprises 41 to 88 per cent of the distance from the snout to the cloacal opening. When incomplete, as it rarely is, there is no evidence that regeneration occurs, as it does in the tail of lizards in most other families.

The limbs are of moderate dimensions; in the outstretched position the distance between the tips of the longest toes measured, respectively, across the chest and the pelvic region, excluding the claws, comprises 63 to 83 per cent of the snout-to-anus length; the fore limbs are approximately the same size as the hind limbs, but are equipped with slightly longer claws. The forelegs are narrowest at their point of insertion, increasing in circumference towards the elbow, flattened at the wrist, and terminating in a broad manus with five digits. The third and fourth digits extend forward to approximately the same level, followed by the second, fourth, and first. The manus, from the base to the tip of the longest toe, is slightly longer than the wrist. The hind limbs are broad at their insertion, tapering towards the knee joint, with the lower limb flattened and increas-

ing in breadth towards the base of the foot. The fourth toe barely exceeds the third, which extends farther forward than the second, the fifth toe being next, with the first, or inner toe, shortest.

SCUTELLATION

The upper surface of the head is covered with large convex scales, each of which is in contact with from four to eight, most often with five, contiguous scales. The scales are thin, horny coverings of osteoderms, which on the top of the skull in adults are fused to the underlying bone. Normally the rostral is nearly twice as broad as high, but sometimes it is divided by a vertical suture on one or both sides to form scales, which, but for their position, are indistinguishable from supralabials. Behind the rostral there are normally two postrostrals, less commonly one or three, or an additional scale may be separated from each of the normal two to make a total of four. Laterally a prenasal and a supranasal are in contact with the outer borders of the postrostrals. Sometimes the scales are irregular, but ordinarily there are two, or rarely three, scales distinguishable as internasals. Posteriorly the supranasal is in contact with the first canthal, which may or may not be in contact with the nasal; behind the first canthal there are normally two, or rarely three, scales, not always in line on the canthus rostralis, but recognizable as canthals nonetheless. Except for their position, these are otherwise indistinguishable from three (rarely two or four, or even a single bar-like scale when the normal three have apparently fused) superciliaries above the orbit. Other scales on the top of the head are too irregular to be designated individually, although there are from six to nine across the head between the posterior superciliaries. Those on the crown fused to the underlying bone are juxtaposed, whereas over the temporal region each scute is surrounded by granular scales (see fig. 1).

On the sides of the head the nostril pierces the anterior portion of a large nasal plate, which is bounded posteriorly by a large postnasal. The upper end of the postnasal may be in contact with the supranasal or the first canthal. There are from two to four loreals between the postrostral and the preoculars, which vary from one to two. In addition to the superciliaries

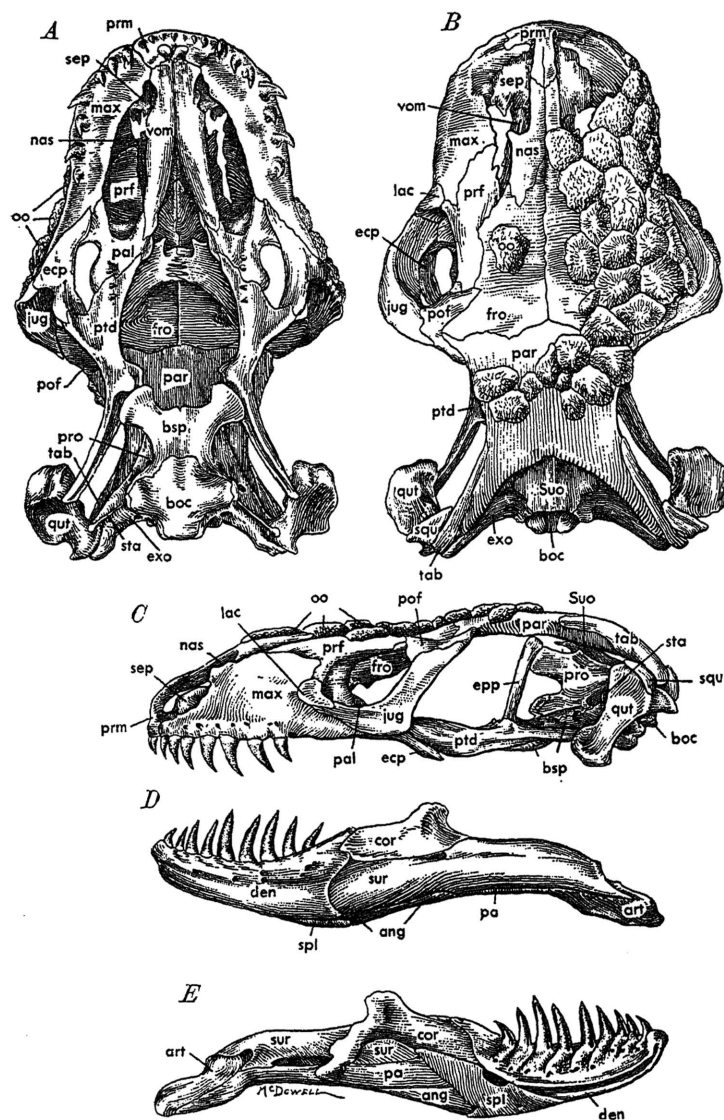


FIG. 1. *Heloderma horridum*. A.M.N.H. No. 57863. $\times 1$. A. Ventral view of skull. B. Dorsal view. C. Lateral view. D. External view of mandible. E. Internal view of mandible. *Abbreviations*: ang, angular bone; art, articular bone; boc, basioccipital bone; bsp, basisphenoid bone; cor, coronoid bone; den, dentary bone; ecp, ectopterygoid bone; epp, epipterygoid bone; exo, exoccipital bone; fro, frontal bone; jug, jugal bone; lac, lacrimal bone; max, maxilla; nas, nasal bone; oo, osteodermal ornamentation of skull; pa, prearticular bone; pal, palatine bone; par, parietal bone; pof, postfrontal bone; prf, prefrontal bone; prm, premaxilla; pro, pro-otic bone; ptd, pterygoid bone; qut, quadrate bone; sep, septomaxilla; spl, splenial bone; squ, squamosal bone of squamatus; sta, stapes; suo, supraoccipital bone; sur, surangular bone; tab, tabular bone; vom, vomer. Drawing by McDowell, after a drawing by Alma Froderstrom.

and the preoculars, there are usually two scales below the eye, and two behind it, one of which may be fused with a subocular.

Below the line extending from the base of the nostril to the lower extremity of the first subocular there are from four to nine lorilabials disposed in one or two rows. The supralabials vary in number from 11 to 15, usually with three of them touching the suboculars. The first supralabial is in broad contact with the rostral, the prenasal, and frequently with the lower posterior corner of the postrostral. The second supralabial may be either larger or smaller than the first, depending upon the presence of a lorilabial that is sometimes wedged in between it and the nasal (or the second supralabial appears to have been split by a suture so that the upper portion becomes a lorilabial). The scales in the temporal region are not differentiated, but there are ordinarily three, and rarely four, in contact with the postoculars.

The ear opening is an oblique slit or an ovoid aperture, the lower end of which is slightly below the level of the corner of the mouth; the second row of scales below the posterior infralabials follows a groove that terminates at the lower anterior extremity of the ear opening, the longest diameter of which is equal to or slightly smaller than the aperture of the eye. There are from three to five tubercular scales anterior to the ear opening, sometimes with a few smaller, flattened scales between them and the membranous lining of the aperture; at its posterior margin from seven to nine rows of smaller scales continue inside the opening to the margin of the tympanum, which may or may not be visible.

The mental is essentially wedge shaped, truncated posteriorly or with a flattened apex, sometimes with the posterior end constricted to produce a "shield-shaped" scale (see fig. 8). The infralabials vary in number from 10 to 17, the first two, or only the first, being in contact with the anterior pair of chin-shields. There are three or four rows of sublabials, with scales intermediate in size between them and the smaller gular scales. From two to four pairs of enlarged chin-shields meet on a median groove. Behind the chin-shields and the sublabials there is a transitional area of slightly enlarged scales, followed by the gulars, which are ovoid, con-

vex, and arranged in diagonal rows. At the gular fold the scales are smaller, in horizontal rows, and separated by granular scales within the groove formed by the fold. Under the pectoral region the scales are flattened, larger than the gulars, somewhat rounded, and irregularly disposed. Posteriorly they merge with flattened, squarish scales arranged in horizontal rows on the venter. At the pelvic region the rows again give way to a narrow area of irregular scales, with or without enlarged preanal scales. The scales beneath the tail are similar to those on the venter, but slightly more angular.

The tuberculate scales of the dorsum of the trunk are so arranged as to be in rows both horizontally and diagonally. Each scale is separated from others by irregular granular scales, which diminish in extent laterally as they approach the flat, squarish, juxtaposed scales of the ventral surface. The scales near the midline are round and relatively uniform in size except in the slight depression above the spine, where a few smaller scales occur; laterally the scales become increasingly ovoid towards the venter where there is a rather abrupt transition to the flattened scales.

On the tail the scales are in horizontal rows and so arranged that they are also in longitudinal rows on the dorsum, but in diagonal rows on the side, with granular scales separating them. The scales may be tuberculate, or nearly conical anteriorly, and ovoid near the tip of the tail.

On the anterior surface of the limbs the scales are convex and irregularly enlarged, with most of them juxtaposed on the fore limbs, but separated by granules on the hind limbs. On the posterior limb surfaces the scales are smaller and separated by granular scales. There is a series of transverse plates on the inferior surface of each digit; these plates are separated from similar plates on the dorsal surface by one or two series of smaller scales on the sides of each digit.

Osteoderms, or bony tubercles, are present on the dorsal and lateral scales of the trunk as well as of the tail, diminishing in size towards the ventral surface, which is devoid of dermal ossifications or retains mere ring-like vestiges, except in the preanal region, where flattened osteoderms are present. They are also present

on the anterior surfaces of the limbs, where they underlie the larger scales.

PATTERN AND COLORATION

The pattern of *Heloderma* varies from population to population and is, moreover, subject to ontogenetic change. Juveniles are distinctly marked, the pattern consisting basically of an irregular dark area on the neck, followed by four dark areas on the trunk, a light area over the sacral region, and from four to seven dark bands on the tail. The dark areas vary in extent, they may be connected or not, and usually include lighter spots. The distal portions of the limbs are dark, usually black, but on the proximal portion of the forearm there is an abrupt change to the lighter color.

In most populations the juvenile pattern is almost completely lost, apparently during the early years of life. The individual undergoes progressive change, usually becoming increasingly darker, with the lighter area of the pattern reduced to vestiges or with only an occasional light bar or spot. Or lighter elements of the juvenile pattern may be retained in varying degrees, usually accompanied by the appearance of lighter areas on portions of the limbs, body, and tail that formerly were black.

The pattern that results is usually a black or dark brown reticulum enclosing lighter spots and bars, or the black may be so extensive as to represent what might be described as the ground color, with lighter circles, dots, or bars usually present, except on specimens from the southern portion of the range, where black

may predominate, with the pattern vestigial in adults. The belly is variously mottled, or irregularly banded in those individuals that retain the cross bars of the juvenile pattern. The dark areas may be either black or various shades of dark brown in adults; the lighter areas vary from a yellowish white to yellow, through various shades of pink, or even red, in individuals from some regions. The fading of specimens in preservative makes it impossible to provide precise information concerning variations in the coloration of these lizards in life.

Heloderma horridum horridum (Wiegmann)

MEXICAN BEADED LIZARD, ESCORPION

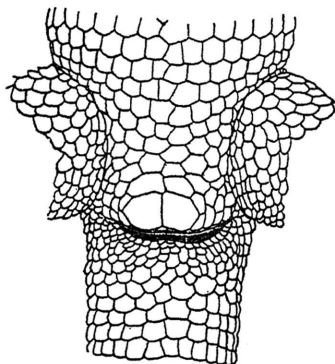
Plates 5-7

Trachyderma horridum WIEGMANN, 1829, Isis von Oken, vol. 22, p. 421.

Heloderma horridum WIEGMANN, 1829, Isis von Oken, vol. 22, p. 628; 1834, Herpetologia Mexicana, pt. 1, pp. 24-25, pl. 1.

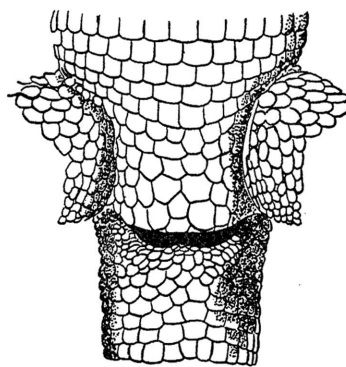
TYPE

A mounted specimen, presumably still present in the Berlin Zoological Museum, that was described and figured by Wiegmann (*supra cit.*). It was collected in "Mexico" by Ferdinand Deppe. Following his diagnosis of *Heloderma*, Wiegmann quotes Hernández as stating that the lizard is "native to the fields of Cuernavaca" ("*Versatur in Quauhnahuacensibus agris*"), where *horridum* is known to occur. In the absence of any more definite state-



H. s. suspectum

FIG. 2. Under side of pelvic region of *Heloderma suspectum*, showing the presence of characteristic enlarged scales anterior to the vent.



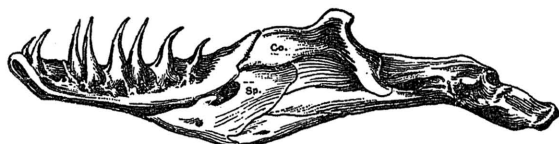
H. h. horridum

FIG. 3. Under side of pelvic region of *Heloderma horridum*, showing the absence of enlarged scales anterior to the vent, as is characteristic of the species.

ment this may be interpreted as an indication of the type locality, or at least as one that might well be designated as such. In view of these facts the type locality is here considered to be Cuernavaca, in the state of Morelos, México.

DIAGNOSIS

At the specific level *horridum* differs from *suspectum*, the only other species in the genus, in having: (1) a tail comprising at least 65 per cent of the snout-to-vent length; (2) 40 instead of 25 to 28 caudal vertebrae; (3) at least 75 rows of subcaudal scales, instead of no more than 62; (4) no pair of enlarged preanal scales (see figs. 2 and 3); (5) the upper posterior process of the splenial not overlapping the coronoid (figs. 4 and 5); and (6) usually two infralabials in contact with the anterior chin-shields (figs. 6 and 7). There are also differences in the dentition, with palatine teeth present in *horridum*, which has six or seven maxillary teeth, in contrast to eight or nine in *suspectum*. At the juvenile stage *horridum* has from six to seven black bands on the tail, including the terminus (which ordinarily is black in both species), in contrast to *suspectum*, the juveniles of which have but four or five. *Heloderma horridum* also attains a larger maximum size than *suspectum*,



H. h. horridum

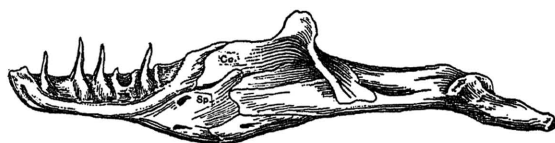
FIG. 4. Lingual view of the right mandible of *Heloderma horridum*, to show the splenial not overlapping the coronoid. Drawing by S. B. McDowell.

and has relatively longer claws in proportion to the snout-to-vent length. There are numerous less sharply defined differences between the species, including the coloration of the head, which is virtually all black on the upper surface in *horridum*, but heavily mottled with pink on *suspectum* except for the snout anterior to the level of the eyes.

At the subspecific level *horridum* may be distinguished from the northern subspecies, *exasperatum* (described below), in having:

(1) the supranasal separated from the postnasal by the first canthal, (2) usually fewer than eight scales across the top of the head between the posterior superciliaries, and (3) usually 11 or fewer scales along the midline of the head between the internasals and the occiput. As an adult *horridum* also tends to have a higher percentage of black or brown included in the pattern of the body.

The pattern and coloration of *H. h. horridum* readily segregate it from *alvarezi*, the subspecies inhabiting the Atlantic drainage of Chiapas; the adults of *alvarezi* are virtually devoid of pattern, with the dorsum almost uniformly slaty black, the venter scarcely mottled,



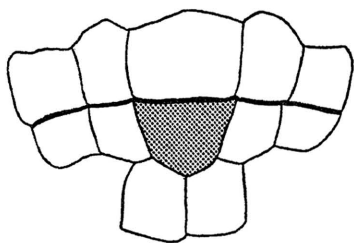
H. s. suspectum

FIG. 5. Lingual view of right mandible of *Heloderma suspectum*, to show the splenial overlapping the coronoid. Drawing by S. B. McDowell.

and with the lighter-colored rings of the tail obliterated or reduced to an occasional light scale or a single row of such scales. Except for Oaxacan specimens, *horridum* may further be distinguished in having a "shield-shaped" mental plate in contrast to the simple wedge-shaped mental of *alvarezi* (see figs. 7-8). *Heloderma h. horridum* apparently attains a considerably larger maximum size than *alvarezi*.

MATERIAL EXAMINED

The following summary is based on an examination of 31 specimens, including 15 males, seven females, and nine of which the sex could not be ascertained because they consisted of stuffed skins, of the head only, or were juveniles with the gonads not sufficiently well differentiated to permit determination of the sex. There is some indication that adult males have slightly longer tails than adult females, and there are other minor differences in proportions. However, there is no apparent difference between the sexes in scale characters, although the series available are inadequate to demonstrate this conclusively. Consequently the sexes have not been treated separately in descriptions

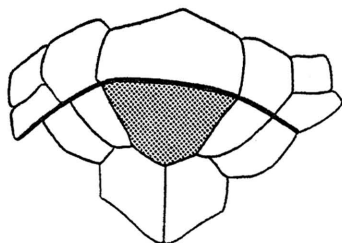


H. s. cinctum

FIG. 6. Diagram of scales on snout of *Heloderma suspectum cinctum*, showing mental scute flanked on each side by first infralabial in contact with anterior pair of chin-shields.

and tabulations of scale characters.

As so often happens when an animal occupies an extensive range, in this instance extending through nearly eight degrees of latitude and representing an elongate area, there are geographic trends in variation. Some areas within the range are much better represented than others in the material comprising the sample studied. Consequently the sample, in one sense, is not truly representative of the subspecies as a whole. It is of some importance, therefore, to point out that more material has been available from the southern portion of the range than from the northern. Listed by states, from north to south, with the number of specimens for each in parentheses, the sample is comprised of the following: Sinaloa (4), Nayarit (2), Colima (2), Michoacán (2), México (1), Morelos (1), Guerrero (7), Oaxaca (10), in addition to two specimens with no more precise locality data than "Mexico," but probably from Guerrero, as nearly as can be inferred from the nature of their



H. h. alvarezii

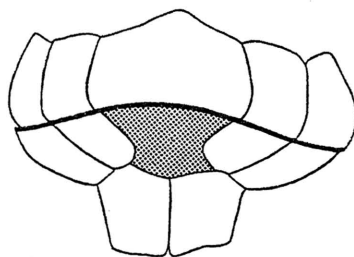
FIG. 7. Diagram of scales on snout of *Heloderma horridum alvarezii*, showing mental scute flanked on each side by the first and second infralabials in contact with the anterior pair of chin-shields.

scutellation and pattern. The description below summarizes the variations encountered; the trends in variation are discussed in a subsequent section.

VARIATION IN THE SAMPLE SERIES

MORPHOLOGY: The description that follows is based on preserved specimens, the few skins and stuffed or mounted specimens being excluded.

The smallest specimen in the series is a juvenile from Montaña de la Gloria, Oaxaca, with a snout-to-vent length of 120 mm. and an over-all length of 204 mm. As noted below, a live specimen we have measured apparently



H. h. exasperatum

FIG. 8. Diagram of snout of *Heloderma horridum exasperatum*, showing the "shield-shaped" mental scute. Compare shape of mental scute with that shown in figure 7.

exceeds in size any specimens known to be preserved. However, the largest complete specimen in any preserved collection is a female (U.S.N.M. No. 46319) from Tehuantepec, Oaxaca, with a snout-to-vent length of 390 mm. and a total length of 690 mm. These dimensions are closely approached by a male (U.S.N.M. No. 1456a) from Ixtepec (=San Gerónimo), Oaxaca, that has a snout-to-vent length of 380 mm., and a total length of 695 mm. A male (L.M.K. No. 33626), with no more precise locality data than "Mexico," but that conforms most closely to individuals from Guerrero, has a snout-to-vent length of 395 mm., thus slightly exceeding both of the Oaxacan specimens. Unfortunately the tail is incomplete on this specimen of uncertain origin so that no over-all dimensions can be given. The head and anterior portion of the trunk, all that were preserved of a large specimen from Tehuantepec, Oaxaca (U.M.M.Z. No. 82417), seemingly represent the largest

specimen with precise locality data that we have been able to examine. The distance from the snout to the anteriormost border of the ear opening is 78 mm. The probable snout-to-vent length of the animal is 410 mm., and the total length would have been close to 745 mm., if it be assumed that the proportions of the specimen approximated those of other adults from the same region. Gadow (1905) mentions having seen a stuffed specimen in the museum at Oaxaca that was "a monster, about 2½ feet [760 mm.] in length." These rough dimensions compare favorably with those calculated on the basis of the head dimensions for the Tehuantepec individual.

However, we have examined an even larger specimen of *H. h. horridum* that was alive in the San Antonio Zoological Garden in July, 1952. In over-all dimensions it exceeds by 5 mm. all other lizards of the species previously seen or reliably reported. It closely approximates the dimensions of the largest specimen of *H. h. exasperatum*, but has a proportionately longer tail, with a slightly (5 mm.) shorter body (snout-to-vent) length.

The weight and measurements of the large *H. h. horridum* captive in San Antonio were obtained through the kindness of the Curator, Mr. John Werler, and his assistant, Mr. Don Darling. This individual had been obtained five years previously from Otto Martin Locke, a dealer located in New Braunfels, Texas, who imports reptiles from México. Many of the reptiles obtained by Mr. Locke come from the Mexican state of Colima, believed to be the approximate source of the enormous specimen we measured. The brown reticulum enclosing lighter, dingy white areas on the body, and the paired black bands on the tail compare favorably with other specimens known to have come from Colima and southern Nayarit. Thus it seems reasonable to believe that the specimen was originally taken in the general region, and quite possibly in Colima.

The specimen (pl. 18, fig. 2) doubtless abnormally fat as the result of its diet and relatively inactive state in confinement, weighed 4358 grams. It had an over-all length of 780 mm. (31.5 inches), with the tail (330 mm.) comprising 73 per cent of the snout-to-vent length, which was 450 mm. The diameter of the tail of this well-fed giant was 76 mm. (3

inches). Unfortunately it was impossible to ascertain the sex of the living specimen. It may be assumed, therefore, that the maximum over-all length does not greatly exceed 780 mm.,¹ although it remains uncertain whether the male or the female attains the maximum size. The snout-to-vent length of the average adult falls between the limits of 325 and 375 mm., with both sexes equally well represented in this range. There seems to be no basis whatever for the statement of Sumichrast (1864a, 1864b) that *horridum* attains a length of "nearly five feet."

The ratio of the tail length to snout-to-vent length varies from 0.80 to 0.88, averaging 0.84, in males, and from 0.72 to 0.80, averaging 0.75, in females. There is thus some indication that females tend to have slightly shorter tails than males. Juveniles, on the other hand, have a tail length to snout-to-vent length that varies from 0.67 to 0.78, with a mean ratio of 0.72, suggesting that ontogenetic changes involve a slight increase in the proportionate tail length in both sexes, with a somewhat greater increase in males than in females. It should be understood that these figures are approximations, even though they are based on the most accurate measurements obtainable from preserved specimens, usually so preserved that they must be measured along the curve of the spine and, whether preserved in alcohol or formalin, may have been subject to differential shrinkage in the body and the tail.

The ratios of the head width to head length

¹After these notes were prepared, Mr. Carl Kauffeld supplied us with a specimen that had been exhibited in the Staten Island Zoo. At the time of its death it had an over-all length of 853 mm., with a tail 375 mm. After preservation in alcohol it had an over-all length of 830 mm., and a tail length of 365 mm., indicating that some shrinkage occurs from the effects of preservation. The specimen is believed to have come from the Mexican state of Colima. Kauffeld reports that a reptile dealer of El Paso, Texas, saw a specimen measured in México that was 39 inches, nearly a meter, in total length. Such dimensions are quite possibly attained even though they are certainly exceptional. Considerable doubt may be still entertained that the species ever attains the 5-foot (ca. 1.5 m.) length claimed for the species by Sumichrast (1864a). Packard (1880) is more nearly correct in his statement that it reaches a length of 1 meter, though wrong in his belief that it is the "largest lizard in Mexico." Dugès (1899) writes that the *escorpión* reaches a length of "un mètre et plus."

of adults vary from 0.74 to 0.87 and average 0.82 in males, and vary from 0.87 to 0.91, averaging 0.87, in females. In juveniles the mean ratio is 0.79, with extremes of 0.72 to 0.87. Here again an ontogenetic change is involved, with an increase in head width relative to the head length from the juvenile to the adult, females tending to have a proportionately broader head than the males. However, when the head length is compared with the snout-to-vent length, it is evident that the juvenile tends to have a head that is somewhat longer in proportion to the body length than is true of the adult, with the male tending to retain a longer head than the female. The ratios of head length to snout-vent length vary from 0.19 to 0.22, with a mean of 0.20, in adult males, and from 0.17 to 0.19, with a mean of 0.18, in adult females, the ratio of juveniles averaging 0.21, with extremes of 0.20 to 0.22.

The maximum span of the hind legs, excluding the claws, comprises approximately 75 per cent of the snout-to-vent length, with no evidence of any significant differences between the sexes or between juveniles and adults. However, there is some indication that proportionately the claws of adults are slightly larger than those of juveniles. The claw of the fourth toe comprises 2.0 per cent of the snout-vent length in juveniles, increasing to 2.4 per cent in adults. The claw of the fourth finger is somewhat larger, averaging 3.0 per cent of the snout-to-vent length in adults, and 2.8 per cent in juveniles.

SCUTELLATION: The scales on the head are subject to minor variations, most of them resulting from the fusion or splitting of the normal complement. The rostral is variable in shape but never divided. The postrostrals are normally two, or they may fuse to form a single broad scale behind the rostral, as on a specimen from Rosario, Sinaloa; two specimens from Chilpancingo, and one from Acapulco, both localities being in the state of Guerrero, have a smaller scale separated from the inferior lateral border of the normal pair of internasals to make a total of four postrostrals. There are normally two internasals, but three are present on a specimen from Sinaloa. The canthals, including the first, which is in contact with the nasal between the supranasal and the postnasal, are almost uniformly

three, four rarely being present. There are usually three superciliaries, rarely fused to form a bar-like scale above the eye, or as many as four may be present. The number of scales between the occiput and the internasals varies from seven to 12, averaging 9.7. Counted across the head between the posterior superciliaries, there are from six to nine scales, usually seven. Most often there are two loreals (66.7%), sometimes one (28.5%), and rarely as many as three (only 4.8%). There are two preoculars, or less commonly one. The supranasal is separated from the postnasal on both sides of all specimens, with the exception of two from Sinaloa, in each of which the two scales are in contact on one side only. The number of lorilabials varies from four to seven, with a mean of 5.1. There are from 10 to 13 supralabials, with 11 the mode, the mean being 11.1; in most instances (65%) the second supralabial does not reach the nasal.

On individual specimens the infralabials invariably exceed the supralabials in number; the infralabials vary from 11 to 15, averaging 13.0, which is also the mode. Normally there are two infralabials in contact with the anterior chin-shields; in some instances (4.5% of the sample) the second infralabial may be separated (on one side only) from the chin-shields by a sublabial. The shape of the mental varies from the northern extremity of the range, where it has lateral indentations along the suture with the first infralabial, to the southern end of the range where the first infralabial on each side is in contact with it along a suture that is only slightly indented. Mental scales intermediate in shape occur in specimens from the central portion of the range. The enlarged chin-shields, counted as pairs that meet on the mental groove and excluding those at the posterior that are separated by small scales, vary from two (in 54% of the cases) to three.

From 51 to 58 scales, the average number being 54.9, can be counted around the body midway between the insertion of the limbs. The number of scales in the first vertical ring around the base of the tail varies from 26 to 35, averaging 29.1. On the under side of the body there are from 59 to 68 scales between the gular fold and the vent (mean, 63.0), and from 45 to 56 (mean, 50.7) rows of scales counted from the axilla to the groin. The number of

rows of subcaudal scales averages 80.2, ranging from 74 to 87. The number of enlarged plates on the inferior surface of the fourth toe varies from 11 to 15, with the mean, 13.1, corresponding closely to the mode (13).

PATTERN AND COLORATION: The nominate subspecies is subject to more variation in pattern and coloration than any other race, probably because it occupies a more extensive range. Aside from the variation encountered in any one locality, there are regional variations. Moreover, the changes in the pattern that occur during the ontogeny further complicate any attempt to describe the various patterns encountered. Photographs of preserved as well as living specimens have been reproduced in plates 5 to 8, which supplement and clarify the descriptions that follow.

Juveniles from various areas more closely resemble one another than do adults. Basically the pattern consists of lighter areas (whitish in alcoholic specimens, yellow in life) comprised of dots, bars, or irregular spots on a black or brown ground color. Usually the pattern is more or less bilaterally symmetrical. The anterior portion of the head, including the lower lips and sometimes the entire throat, is black or brown. Light dots are sometimes present on the occipital region, and slightly larger spots are present posteriorly on the upper, as well as on the under, side of the neck. A light area immediately anterior to insertion of the foreleg is variable in extent; it may completely encircle the proximal end of the limb, and sometimes the right and left sides of the light area are connected by a light bar across the chest. Usually the fore limbs are dark, sometimes with blotches on the forearm. Commonly there is a spot, five to 12 scales in extent, above the insertion of the limbs or on the neck. This is the first of a series of from three to six light spots in a row at the center of the back. On the sides there are usually three, sometimes four, conspicuous light bars that are from three to six scales in width. The position of each bar roughly coincides with a spot at the middle of the back, much as though a light bar extending across the body had been interrupted on each side. The bars are separated from one another and from the spots on the dorsum by the dark ground color, which is interrupted at intervals by smaller spots that are

irregular in shape. The light bars extend onto the edges of the belly, which is otherwise characterized by having an irregular but roughly bilaterally symmetrical pattern in which either the light or the dark color may predominate.

A light bar usually extends across the sacral region to the base of each hind limb, often with an abrupt change near the middle of the femoral portion of the limbs to the dark coloration of the distal portion, which is black or brown anteriorly but blotched with light on the posterior side. Behind the light bar across the sacrum there is a dark band on the base of the tail, with the remainder of the appendage encircled by from five to six light areas that alternate with five, or rarely six, additional dark areas, including the tip of the tail, which is invariably dark. [The juvenile depicted in color by Günther (1885) is fairly typical, but larger blotches ordinarily present in the median row on the back are lacking above the chest and neck.]

Such patterns are characteristic of seven juveniles that are from 205 to 235 mm. in total length. There is no proof, but presumably these represent animals in their first year of life. A slightly larger specimen from Acapulco with a total length of 246 mm. seems already to have undergone some change. Three or four dark scales are present in each of the light spots on the midline of the trunk, and a few dark scales, some in rows, appear in the light bars. Such changes probably occur during the latter part of the first year. Later in life, possibly during the second or third years, black scales, most of them in rows, begin to appear near the middle of each light band encircling the tail. As the change proceeds during ontogeny the black scales increase in extent to form a broad black band that separates two narrow light bands, the vestigial portions of each broad light band of the juvenile. Each original black band continues to broaden, to include the contiguous rows of scales that were light in the juvenile. The resulting pattern consists of five (less commonly six) pairs of narrow light stripes on a black tail. In some specimens either one or two light bands, or partial bands, appear in the middle of most of the dark bands. Patches of lighter scales also appear on the limbs in areas that were formerly black or brown, and the light spots on the dorsum ap-

pear to have become larger and more numerous. By the time the individual has attained an overall length of 380 mm. (see pl. 6), only a few vestiges of the juvenile pattern remain, and on fully adult specimens from some areas virtually all trace of the juvenile pattern is obliterated.

The most complex patterns occur in eastern Oaxaca, where mature specimens are dark brown mottled with yellow. A similar pattern is represented on a specimen from southern Sinaloa, however, although other specimens from the same general region are more aptly described as dark brown with small yellow spots rather widely scattered over the body. Adult individuals from many parts of the range retain one or more of the light circles along the vertebral line, especially towards the sacral region. Vestiges of the lateral light bars are still apparent on some specimens from Guerrero, Morelos, and Michoacán. Often they consist of a light yellow or a pink or reddish pattern that sharply contrasts with a ground color that is nearly coal black. The most extreme pattern is encountered on one specimen from Chilpancingo, Guerrero; this individual is almost uniformly black, with only a few light spots composed of one or two or as many as eight scales. This specimen represents the nearest approach to the almost uniformly dark, virtually patternless subspecies *H. h. alvarezi*. However, the complex, rather ill-defined pattern to be seen on some specimens of *H. h. horridum* from the vicinity of Tehuantepec more closely resembles the pattern discernible on half-grown specimens of *alvarezi*.

HABITAT

It seems doubtful whether *H. h. horridum* is restricted to any particular habitat. Sumichrast (1864a, 1864b, 1869) whose observations are not always reliable, states that it "inhabits exclusively the hot zone which extends from the western slope of the Cordilleras to the shores of the Pacific. . . . Its conditions of existence confine it to hot and dry localities, such as the districts of Jamiltepec, Juchitán, and Tehuantepec." He notes further that "it is usually in holes of greater or less depth, dug at the roots of trees or under a mass of vegetable debris," and that this reptile is to be sought "in dry spots on the margins of woods, or in old clearings, the soil of which is covered with vegetable debris, with rotten trunks and grasses." Cuesta

Terrón (1930) says approximately what Sumichrast reports, presumably basing his remarks on the earlier statements.

On the other hand, Hartweg and Oliver (1940), who obtained two specimens, one from Quiengola Mountain and the other from the Cerro de Mixtequilla, both on the Pacific side of the Isthmus of Tehuantepec, note only that the species was "not common," and "never observed on the plains." Earlier in their paper they point out that "the vegetation of the Tehuantepec region consists mainly of spiny scrub and of many varieties of cacti, with a few large trees interspersed," whereas "The vegetation on Quiengola Mountain differs from that about Tehuantepec mainly by the greater abundance of trees and the consequent shading out of the smaller plants of the plains proper." Mr. Paul D. Rühlking, who collected a specimen "west of Mixtequilla" in the same general region records in his field notes that the specimen was taken "in a hole in sloping bank near a swamp."

Farther north, in Guerrero near the Morelos border, H. M. Smith (1935) reports that a large specimen taken on the road at night was in a habitat that consisted of "grass and deciduous trees." Similarly, Gadow (1930) observes that, at least in Michoacán, *H. h. horridum* prefers "woods, or fairly wooded localities with soft soil, preferably humus." Oliver (1937) notes that a specimen of *horridum* taken at Paso del Río in Colima was "found in a wooded area," and he describes the area as a "coastal region, which is characterized by dense vegetation and much humidity. There are numerous swamps and lagoons surrounded by thick hardwood forests, open scattered patches of savanna grassland, and a few arid portions with cacti and other xerophytic plants."

In southern Sinaloa, where *horridum* has thus far been taken only on the coastal plain, the terrain in the vicinity of Presidio, the source of the specimen reported by Boulenger (1885), is described by Taylor (1938b) as "flat, with low forest." The same description would apply to the area 12 miles north of Rosario, where the senior author collected a specimen of *horridum* on November 21, 1939. This adult individual was crossing the road in an area sparsely covered with thorn forest composed of relatively small trees.

If one may judge by Leopold's (1950) excellent map of the vegetation of México, the

range of *H. h. horridum* extends through regions that are predominantly tropical deciduous forest or thorn forest. Under specialized local conditions the species may occur in regions mapped as savanna, or pine-oak forest. According to the Thornthwaite (1931) classification, the climates of all the areas occupied by *horridum* are characterized by a winter deficiency in rainfall, but range from humid to subhumid, in temperature provinces that vary from tropical to microthermal. There are no records for *Heloderma* in the wettest portion of the Pacific coast of México, where heavy rains occur in all seasons, in northwestern Jalisco and western Nayarit, and it is not impossible that *Heloderma* is absent from the area.

The biotic provinces of México as mapped by H. M. Smith (1940, 1949), Moore (1945), and Goldman and Moore (1945) may have some validity for other groups of animals, but they are meaningless as far as the distribution of *Heloderma* is concerned.

RANGE

Heloderma h. horridum occupies an area on the Pacific drainage of México that extends from southern (and probably central) Sinaloa southeastward to extreme eastern Oaxaca at the Isthmus of Tehuantepec. Near the central portion of this area *horridum* occurs along the coast as well as approximately 275 kilometers (171 miles) inland in the states of Jalisco, Michoacán, México, and Morelos. Altitudinally the range extends from sea level to at least 1500 meters (nearly 5000 feet) and possibly to 2000 meters.

LOCALITY RECORDS

The specimens listed by museum number have been examined. Locality records of specimens reported by others but not examined by us are included in the list, with their source indicated. Approximate elevations in meters for each of the localities are indicated in parentheses following the name of the town. The record for "Guanajuato" credited to Dugès by Günther (1885) is doubtless based on a specimen shipped to Europe from Guanajuato by Dugès, who never recorded any specimen from the state himself. Also, it is virtually certain that *Heloderma* does not occur in the state of Veracruz, although Cuesta Terrón

(1934) reported a specimen said to have been seen in the Sierra de Zongolica. Later a specimen obtained in the general region and reputed by the local natives to be a venomous *escorpión* proved to be *Xenosaurus grandis* when examined by the junior author. Reports of *escorpiones* in other parts of México usually prove to be based on gerrhonotine lizards.

The records for Etúcuaro (Gadow, 1930) and Puruarán (Dugès, 1896), both in Michoacán at elevations of 1800 meters and 2000 meters, respectively, higher than any other localities reported, may possibly be open to question, but there is no reason to doubt the reliability of others on the list that follows. (See map 2.)

SINALOA

- Piaxtla, "80 km. n. of Mazatlán" (75 m.), U.I.M.N.H. No. 34932
- Presidio (50 m.), Boulenger, 1885, p. 302
- 12 miles northwest of Rosario (100 m.), A.M.N.H. No. 62348
- Escuinapa (100 m.), A.M.N.H. No. 618, M.C.Z. Nos. 7012, 7013

NAYARIT

- "Between San Francisco and Santa Teresa" (1000 m.), A.M.N.H. No. 7216
- Jesus María, A.M.N.H. Nos. 74940, 74941 (received too late to map)
- Mesa de Nayarit, A.M.N.H. No. 74943 (received too late to map)
- Huajimic (1500 m.), M.C.Z. No. 6935

JALISCO

- Barranca de San Cristóbal (800 m.), Dugès, 1896, p. 480
- Autlán (900 m.), Dugès, 1896, p. 480

COLIMA

- Colima (480 m.), H. M. Smith, 1939a, p. 316
- Paso del Río (100 m.), U.M.M.Z. No. 80142, C.N.H.M. No. 1675

MICHOACÁN

- Etúcuaro (1800 m.), Gadow, 1930, p. 52
- "Parécuaro" = Parácuaro (600 m.), Gadow, 1930, p. 52
- Apatzingán (682 m.), C.N.H.M. No. 37142
- Puruarán (2000 m.), Dugès, 1896
- Oropeo (300 m.), Gadow, 1930, p. 52
- Coalcomán, Sierra de la Piedra Agua (1076 m.), J. A. Peters, 1954, p. 19
- 2 miles northeast of La Placita = Sulatillo (20 m.), U.M.M.Z. No. 101468

MÉXICO

Tejupilco or Texulpilco (1400 m.), M.V.Z.
No. 16434

MORELOS

Cañon del Lobo, near Cuernavaca (1538 m.),
M.N.H.N.M., not numbered

GUERRERO

Haujintlán (1000 m.), E.H.T.-H.M.S. No.
31383 (formerly E.H.T.-H.M.S. No. 773,
reported from "11 miles southwest of Puente
de Ixtla" by H. M. Smith, 1935, p. 145)
Placeres de Oro (Arroyo del Vizcaino, 400
m.), I.B.M., not numbered
Chilpancingo (1360 m.), C.N.H.M. Nos.
38532, 38533
Laguna Coyuca (0+ m.), A.M.N.H. No.
66074
Acapulco (0+ m.), L.M.K. No. 36279
"Guerrero," A.M.N.H. No. 617

OAXACA

Jamiltepec (240 m.), Sumichrast, 1864a, p. 1
Bisilana (100 m.), A.M.N.H. No. 68149
La Concepción (100 m.), U.I.M.N.H. No.
3764
Tehuantepec (100 m.), U.S.N.M. No. 46319
West of Mixtequilla (100 m.), A.M.N.H. No.
19384
Cerro de Mixtequilla (200 m.), U.M.M.Z. No.
82418
Quiengola Mt., 8 kilometers northwest of
Tehuantepec (200 m.), U.M.M.Z. Nos.
82416, 82417
Iztepec = San Jerónimo (100 m.), C.N.H.M.
No. 1456 (2 specimens)
Salina Cruz (100 m.), Boulenger, 1891a, p. 111
Juchitán (100 m.), Sumichrast, 1864a, p. 1
Tapanatepec (280 m.), M.C.Z. No. 27899

***Heloderma horridum exasperatum*,**
new subspecies

RÍO FUERTE BEADED LIZARD, ESCORPIÓN
DEL RÍO FUERTE

Plate 8, figures 3 and 4

Heloderma horridum, BOGERT AND OLIVER,
1945, Bull. Amer. Mus. Nat. Hist., vol. 83, p.
349 (specimens from Alamos and Guirocoba,
Sonora, listed).

TYPE

Number 63699, an adult male, in the collection
of the American Museum of Natural History.
The specimen was collected near the village of
Guirocoba by John W. Hilton during the fall

of 1941. Guirocoba is located on a ranch by
the same name and lies at an approximate ele-
vation of 450 meters on the Río Fuerte drain-
age in the foothills of the Sierra Madre Occi-
dental near the extreme southeastern corner of
the state of Sonora, México.

DIAGNOSIS

This subspecies of *Heloderma horridum*
differs from *H. h. alvarezi* as well as from the
nominate race, to which it is most closely
allied, in virtually always having the supranasal
in contact with the postnasal, rather than sepa-
rated by the first canthal (see figs. 10-11).
Heloderma h. exasperatum also tends to have
more scales (eight rather than six or seven) on
the top of the head between the superciliaries,
and the second supralabial is always in contact
with the nasal or prenasal plates (in only 35%
of *horridum*, never in *alvarezi*). It also differs
from *alvarezi*, which as an adult usually has
a nearly uniformly slaty black coloration, in
contrast to the complex pattern of *exasperatum*,
the only race in which the extent of the light
(yellowish or pinkish) color of the pattern on
the trunk and tail of the adult equals or ex-
ceeds the black or dark brown. In adult *alvarezi*
the light bands of the tail are retained as faint
vestiges, usually discernible in five pairs on the
under side of the tail, with all or most of the
dorsum black. In adult *horridum* there are
either solid dark bands between the five or six
pairs of light rings (pl. 6, fig. 3), or each
dark band may be interrupted by a single light
band, often incomplete (see pl. 7, figs. 1 and 2).
However, in adult *exasperatum* each black
band separating the pairs of light bands is in-
terrupted by two light bands (sometimes im-
perfect) as can be seen in plate 8 (fig. 3).
Whereas juvenile *exasperatum* (a post-juve-
nile only is available) apparently emerges from
the egg with seven (less commonly six) dark
bands, including the tip of the tail, alternating
with six (or five) light bands, the ontogenetic
changes involving the splitting of each light
band by a dark band, and of each dark band
by two light bands, result in a pattern that con-
sists of numerous narrow, light bands, alternat-
ing with almost equally narrow dark bands.
The results of the ontogenetic changes in the
tail pattern of the three races are discussed in
a subsequent section dealing with clines within

the species. Figure 15 depicts idealized patterns that will clarify the present discussion.

DESCRIPTION OF THE TYPE

An adult male, with an over-all length of 585 mm.; snout-to-vent length, 340 mm. The tail, which is 245 mm. in length, comprises 72 per cent of the snout-to-vent length. The distance between the tips of the longest toes (excluding the claws) when the hind legs are outstretched is 240 mm. The distance measured from the base of the claw of the longest digit across the chest to a similar point on the opposite side with the limbs outstretched is 230 mm. The claws measured in a straight-line distance between the point and the dorsal attachment reach a maximum length of 8.4 mm. on the fingers and 6.4 mm. on the toes.

The head is 56 mm. wide at the temporal region and 37 mm. in width across the top at the level of the posterior superciliaries. The distance between the top of the snout and the upper end of the ear opening is 60 mm., from the end of the lower jaw to the gular fold there is a distance of 88 mm.

The rostral is wider than high, in contact laterally with the first supralabial on each side, and with the pair of postrostrals above. The lateral edges of the postrostrals are in contact with the prenasal and the supranasal and followed posteriorly on the snout by a pair of internasals. The upper posterior corner of the supranasal on each side extends backward above the nasal plate to form a suture with the upper end of the postnasal. There are three canthals, the anteriormost lying above the suture of the supranasal and the postnasal. There are two preoculars (with a small round scale between them and the eye), three suboculars, and two postoculars. There are eight scales across the head between the posterior superciliaries, and from 12 to 13 scales between the internasals and the occiput, the count being made along the main axis of the head to a point at the level of the ear opening.

There are 10 supralabials on the right, 11 on the left, the second in each instance being barely in contact with the nasal. The lorilabials are also asymmetrical, with four on the right and five on the left, the anteriormost being the largest in each row, and in broad contact with the nasal.

The infralabials number 12 and 13, the anterior two touching the first pair of chin-shields. The mental is "shield-shaped" (fig. 8), broad at the upper end, with a constriction in the outline near the middle, where it is in contact with the first infralabial on each side. There are four rows of sublabials, the scales at the posterior end of each row progressively diminishing in size and merging with the gular scales. The chin-shields are disposed as three pairs, the right and left member of each pair meeting on the mental groove. A fourth pair is separated by two gular scales at the rear end of the mental groove. Rows of sublabials extend from each of the pairs of chin-shields.

On the under side of the body there are 62 rows of scales between the gular fold and the vent, 49 between the axilla and the groin, and 82 rows of scales beneath the tail between the vent and the terminus. Sixty scales can be counted following one row around the middle of the body, and there are 30 in the first complete row of scales around the base of the tail. There are 13 enlarged plates on the under side of the fourth toe on each side.

The anterior portion of the head is dark brown, almost black, on the flat scales on the snout, including the upper and lower lips. The temporal region and the upper surface of the neck are slightly paler, and without pattern, although a few lighter (yellowish) scales are present on the sides of the neck. On the back there is an irregular network of dark brown to blackish scales enclosing lighter areas, which are indescribably variable in shape (pl. 8), but tending to be angular on each side of the vertebral ridge and to resemble bars on the flanks. From the sides as well as from above, the tail is unevenly banded, with approximately 21 light bands distinguishable, and with the alternating black bands tending to be somewhat wider. All four limbs, including the digits, are irregularly marbled with dark brown and yellow. The coloration of the under side is generally paler than the dorsum, with a few slightly colored scales below the neck and more on the chest. The venter is largely pale brown, with a sort of network of brown lines, some of them diagonal, some horizontal. There is a patch of yellowish scales on the under side of each femur, with a few brown scales scattered through it. The under side of the tail is paler

than the upper, with so little contrast between the light and dark that it is impossible to count the lighter bands, although some rows of scales are pale yellow, particularly near the distal end.

MATERIAL EXAMINED

The sample available consists of 10 males, five females, and one incomplete skin, all presumed to be adults, with the exception of a small male, scarcely beyond the juvenile stage, with a snout-to-vent length of 220 mm. This is the smallest specimen in the series and probably was in its second or third year at the time of capture. All specimens are from three localities in the Río Fuerte drainage basin of southern Sonora and northern Sinaloa.

VARIATION IN THE SAMPLE SERIES

MORPHOLOGY: The sample does not include a sufficient number of size groups for regression curves to be plotted or calculated on a meaningful basis. Also, the series is inadequate to demonstrate with certainty that there is any significant difference in either proportions or scutellation between the adults of the two sexes. Minor differences in proportions are noted for what little value they may have.

The smallest specimen is a post-juvenile male 390 mm. in length, with a snout-to-vent measurement of 220 mm., the tail length (170 mm.) comprising 77 per cent of the distance from the snout to the vent. The largest specimen is a male from Guirocoba with an over-all length of 775 mm., a snout-to-vent length of 455 mm., and a tail that is 320 mm. long. Half of the adult specimens in the sample fall within a range of 325 mm. and 375 mm. for snout-to-vent length. The ratio of the tail to the snout-to-vent length is 0.70. The same ratio varies from 0.70 to 0.77, averaging 0.76, in adult males, and from 0.71 to 0.74, averaging 0.73, in adult females. These data suggest that males tend to have tails that proportionately are slightly longer than those of females.

The ratio of the head width to head length varies from 0.77 to 0.95 in both sexes, with means of 0.90 for males and 0.88 for females. The head length comprises approximately 18 per cent of the snout-to-vent length, varying from 16 to 20 per cent, with a tendency for males to have slightly longer heads proportionately than females. The average span of

the outstretched hind legs comprises approximately 75 per cent of the snout-to-vent distance, with no indication of any difference between the sexes. The claws of the fourth finger average 2.8 per cent of the snout-to-vent length, being somewhat larger than those on the fourth toe, which average but 2.1 per cent.

SCUTELLATION: The rostral is uniformly undivided, whereas the postrostrals vary from the normal two (present on 73.3%) to three (20%) or, on one specimen, as many as four. There are normally two internasals, rarely three. The canthals may be represented by two scales (23%), or rarely by as many as four (7%), but normally there are but three. Usually there are three superciliaries, less commonly two, and rarely as many as four. All specimens in the sample have eight scales across the head between the posterior superciliaries. The scales behind the internasals, counted along the middle of the head to the level of the ear opening, vary from 10 to 12, averaging 10.9.

On the sides of the head there are commonly two loreals (in 57% of the cases tabulated), sometimes three (33%) or only one (10%). The lorilabials are restricted to a single row, or occasionally one may be split horizontally; they vary in number from four to six, averaging 4.5. There ordinarily are two preoculars, or rarely only one. The supranasal is in contact with the postnasal in all cases, with the exception of the post-juvenile, where it is barely separated on the right side only. Usually there are 11 supralabials, but the number varies from 10 to 13, averaging 11.29. The second supralabial is always in contact with the nasal or the prenasal, usually with both.

The number of infralabials varies from 12 to 15, averaging 13.5, with the anterior two in contact with the first pair of chin-shields on 13 specimens of the 15 examined. The mental shield is wide at the lip, but constricted laterally in outline along the suture of the first infralabial. There are always three pairs of chin-shields along the mental groove, usually with a posterior fourth pair, the individual scales of which are separated from the groove by smaller scales.

The number of scales around the body midway between the limbs varies from 54 to 60, averaging 56.8. There are from 27 to 34 scales in the first vertical ring around the base of the tail, the mean number being 30.3. The number

of scales between the gular fold and the vent varies from 61 to 73, averaging 65.3. Between the axilla and the groin there are from 49 to 57 rows of scales, with 51.9 as the mean. The number of rows of scales posterior to the vent on the under side of the tail varies from 77 to 85, the mean number being 80.4. There are from 12 to 15 plates on the under side of the fourth toe, with 14 as the mode and 13.7 the mean.

PATTERN AND COLORATION: The majority of the specimens comprising the sample are essentially similar to the type in both the color and markings. On some of the paratypes the areas of light color on the trunk exceed the black in their extent. This is particularly true of the larger specimens, where the light color of the pattern appears to have been pink in life. In many respects the pattern on the trunk of the Sonora population more closely resembles that of *H. s. suspectum*, the species to the north, than it does that of *H. h. horridum*, although anterior to the sacral region a few specimens are marked with light-colored rings enclosing a black dot, the target-like markings characteristic of a high percentage of the specimens belonging to the nominate subspecies.

The complex pattern on the tail, with numerous light-colored rings alternating with black rings, is rather distinctive, although it is simulated in a few specimens of *H. h. horridum*. In the series of *exasperatum* obtained in Sonora, from 18 to 25 light rings can be counted on the tail (a single somewhat faded specimen from Sinaloa has a tail with a mottled pattern separating five pairs of narrow, light rings). On freshly preserved specimens it is apparent that there is an alternation of one light band with two bands that are slightly darker. Unfortunately no juvenile specimens of *exasperatum* have been taken, but it seems probable that they do not differ appreciably from those of *horridum*. To judge by the adults, juveniles in the Río Fuerte drainage usually have six, less commonly five, light bands on the tail. It may be inferred that the ontogenetic changes that occur involve (1) a progressive broadening of each dark band, accompanied by (2) the appearance of two paler bands within each dark one. Thus, while adult *H. h. horridum* has either five pairs of light rings, with or without one light ring in the center of each intervening black ring, or a total

of five pairs or triads of light tail rings, an adult of *exasperatum* has five or six quadrads, or a total of at least 20 light rings, although the bands are rarely perfect and may be represented by mottled areas. The light bands that appear in the original black band of the juvenile are somewhat larger than the vestigial ends of the original light bands. Thus vestiges of the juvenile tail pattern are still discernible, although on some specimens the banding is too irregular to conform precisely to the ideal situation described (and depicted in fig. 15).

The higher percentage of the lighter color on the tail of *exasperatum* as compared with *horridum* is in keeping with the generally paler color on the body, although there is no appreciable difference in the coloration of the head.

HABITAT

Heloderma h. exasperatum occurs along the northern periphery of the Barranca region, defined by Gentry (1942) as the "precipitous belt along the coast [of México] in which the rivers have eaten back into the central plateau." If Gentry's designations be used, the Río Fuerte beaded lizard is probably most abundant in the Short-tree Forest, possibly ranging into the Oak Forest at higher elevations, or into the Thorn Forest below. Gentry defines the Short-tree Forest in southern Sonora as "a heterogeneous deciduous forest with a strong infusion of tropical elements," lying principally in the canyons or barrancas between the elevations of 1000 and 3500 feet above sea level. In the region around Alamos, where the subspecies is not infrequently encountered during the summer rainy season, the annual rainfall is 708 mm. (nearly 28 inches), with the maximum precipitation during the months of July and August. The dry season occurs during March, April, and May, with scarcely any rain during April (Arias, 1942). (See pl. 14, fig. 2.)

RANGE

At present *H. h. exasperatum* is known to occur only in the drainage basin of the Río Fuerte in extreme southeastern Sonora and the adjacent portion of Sinaloa. It is virtually certain that the subspecies ranges eastward into the barrancas of western Chihuahua, and it is probable that it will be found to the north in the drainage basin of the Río Mayo. As far as

present records indicate, there is a considerable hiatus between the range of *exasperatum* and that of the nominate subspecies to the south. Nonetheless, it is probable that *exasperatum* occurs, possibly in more or less isolated populations, in most of the barrancas of central Sinaloa; specimens of *H. h. horridum* from the southern portion of the state have the supranasal in contact with the postnasal, as is characteristic of *horridum* farther south. However, the supranasal and the postnasal are so narrowly in contact in the Sinaloan specimens of *H. h. horridum* as to suggest that actual intergradation with *exasperatum* is to be found in populations not far north of Mazatlán. It is doubtful whether *exasperatum* occurs on the narrow coastal plain, but collectors of the future may provide the evidence to belie this assumption.

LOCALITY RECORDS

The majority of the specimens were obtained at Guirocoba and Alamos in southern Sonora. One specimen was taken at a lower elevation, virtually on the edge of the narrow coastal plain of northern Sinaloa. Through the courtesy of Dr. and Mrs. Charles Vaurie we have seen a photograph of a specimen taken at Minas Nuevas, and on this basis we include the locality within the known range. The specimens listed below, in addition to the type, may be considered paratypes. The figures in parentheses refer to the approximate elevation in meters of the localities listed.

SONORA

Minas Nuevas (record based on photograph)
Alamos (450 m.), A.M.N.H. Nos. 64220-64224

Guircoba (450 m.), M.V.Z. Nos. 50863-50866, A.M.N.H. Nos. 63698, 63699 (type), 63700-63703

SINALOA

San Blas (100 m.), U.S.N.M. No. 38116

Heloderma horridum alvarezii, new subspecies

CHIAPAN BEADED LIZARD, BLACK BEADED
LIZARD, OR ESCORPIÓN NEGRO

Plates 3 and 4

Heloderma horridum, SMITH AND TAYLOR,
1950, Bull. U. S. Natl. Mus., no. 199, p. 193
(part, one Chiapas record listed).

TYPE

A specimen in the collection of the Instituto de Biología, Universidad Nacional Autónoma, México City, México. It was collected in the immediate vicinity of Tuxtla Gutiérrez, Chiapas, by Señor Miguel Alvarez del Toro, in whose honor it is named.

DIAGNOSIS

A subspecies in which the pattern is almost completely lost during the early years of the life of the individual. Only the barest vestiges of the lighter areas of the juvenile pattern are retained by adults, the dorsum of which is slaty black, and nearly uniformly so, in contrast to other subspecies of *horridum*, fully grown specimens of which retain well-defined patterns. As far as can be ascertained, *alvarezii* does not attain the maximum size reached by individuals of other subspecies.

There are no marked differences in scutellation between *H. h. alvarezii* and *H. h. horridum*, its closest relative. There is a general tendency for *alvarezii* to have fewer scales, but most of the differences barely approach statistical significance, suggesting only that the Chiapas population represents the southern segment in a cline that extends along the Pacific drainage from Sonora to Chiapas.

DESCRIPTION OF THE TYPE

A subadult female, with the habitus and the general arrangement of the scales similar to those of the nominate subspecies. The over-all length of the specimen is 462 mm., of which the body and head comprise 258 mm. and the tail 204 mm. The tail comprises 79 per cent of the snout-to-anus length. At the temporal region, where it is widest, the head has a diameter of 39.5 mm.; at the eye level the diameter is 31 mm. The head length from snout to the anterior border of the ear opening measures 41 mm.

There are a pair of postrostrals and a pair of internasals. The supranasal is separated from the postnasal by the first canthal. The loreal is single on each side. There are two preoculars, three superciliaries, two postoculars, and two suboculars surrounding the eye. The supralabials are 10-11, the infralabials 12 on each side. The mental is somewhat less than

twice as broad as high, with the lateral edges at an acute angle with the labial border and slightly curved along their suture with the first infralabial. Posteriorly the mental is followed by three pairs of enlarged chin-shields that are in contact on the median line. The first enlarged chin-shield on each side is in contact with two infralabials and the anterior sublabial.

There are 60 scales between the gular fold and the cloacal opening, and 50 rows of flattened ventrals between the levels of the axilla and groin. On the under side of the tail there are 76 rows of scales. Counted transversely, around the middle of the trunk there are 53 scales, and around the base of the tail there are 26 scales. There are 13 enlarged, flattened scales on the under side of the fourth toe.

The general coloration is blackish or slaty black, bordering on dark brown. There are vestiges of yellow markings on the belly and on the inferior surface of the tail, where indistinct cross bars represent the light rings of the juvenile pattern. The pattern is almost completely obscured on the dorsum (see pls. 3 and 4).

MATERIAL EXAMINED

The sample comprises two adult males, an adult female, three subadult females (including the type), and one partly grown juvenile, the sex of which cannot be ascertained with certainty. All seven specimens are from five localities on the headwaters of the Río Grijalva (or Río Chiapa), which flows into the Atlantic in the Mexican state of Chiapas. The type and other specimens that may be considered paratypes are listed below.

VARIATION IN THE SAMPLE SERIES

MORPHOLOGY: There are too few specimens to determine whether there are any differences between the sexes in the proportions or in scutellation. Certainly there is no simple means of ascertaining the sex without examination of the internal anatomy. The series provides some indication of ontogenetic changes in proportions. However, the nature of these changes cannot be established until more material is available.

The smallest specimen is a post-juvenile with an over-all length of 236 mm. and a tail 93 mm. long that comprises 65 per cent of the

snout-to-vent length, which is 143 mm. The largest, and incidentally the darkest, specimen is an adult male from Cintalapa, Chiapas. This individual has an over-all length of 650 mm., a snout-to-vent length of 355 mm., with a tail 295 mm. long that comprises 83 per cent of the snout-to-vent length. The next largest specimen is a female with an over-all length of 635 mm., although the tail comprises but 74 per cent of the snout-to-vent length. In view of the fact that the juvenile has a tail that is proportionately the shortest in the series, whereas the largest male lies at the opposite extreme, it seems probable that the tail increases in length somewhat more rapidly than the head and body. The ratio of the head width to head length is approximately 0.86, with minor variations in adults, whereas the single juvenile has a proportionately narrow head, with a width to length ratio of 0.77. The head length comprises approximately 18 per cent of the snout-to-vent length. It was impossible to obtain reliable measurements of the hind leg span in most instances, but the distance between extremities of the toes (excluding the claws) comprises approximately 65 to 70 per cent of the snout-to-vent length. The longest claws on the fingers average 2.6 per cent of the snout-to-vent length, those on the toes being somewhat shorter, or 2.0 per cent.

SCUTELLATION: The variations encountered in the sample representing *alvarezi* are not so extensive as they are in the other two races of *horridum*. Although *alvarezi* occupies a limited range in Chiapas and the population is probably isolated from *horridum* in Oaxaca by the continental divide, the apparent uniformity in scutellation can probably be attributed more to the small size of the sample than to the lack of variability.

The rostral is undivided, slightly less than twice as broad as it is high, and roughly quadrangular in shape, with a slight upward projection between the postrostrals, which are regularly paired. There are always two internasals and nearly always three canthals, although the smallest specimen has but two on the left side. There are usually three superciliaries, rarely one. There are commonly six, rarely seven, scales separating the posterior superciliaries across the top of the head. Counting down the approximate middle of the head

there are from seven to nine (mean 8.4) scales between the internasals and the occiput, at the level of the ear opening.

The loreal is commonly single, but nearly as often represented by two scales, never by three. Without exception the supranasal is uniformly separated from the postnasal by the first canthal, which is in broad contact with the nasal. There are from four to five, usually five, lorilabials, always in a single row. Without exception the first lorilabial is situated beneath the nasal, thus preventing it from touching the second supralabial. Two preoculars are always present. Usually there are 11 supralabials, less commonly 10, with the first one larger than the others, and the upper half of the second split off to form the first lorilabial.

There are from 11 to 14 infralabials, averaging 12.2, the first two of which are invariably in contact with the mental. The mental is scarcely if at all constricted in outline where it touches the infralabials, being essentially wedge-shaped, but truncate posteriorly or with a slight apex at the contact with the first pair of chin-shields. Of the three pairs of chin-shields, the right and left scales of all, or less commonly of but two, meet at the mental groove.

The number of scales around the middle of the trunk varies from 49 to 56, the mean number being 52.4. The number of scales in the first complete annulus around the base of the tail behind the vent varies from 24 to 31, averaging 26.3. There are from 60 to 67 (mean 62.1) scales between the gular fold and the vent, and from 48 to 50 rows of the scales on the belly between the axilla and the groin. The rows of scales on the under side of the tail between the vent and the tip vary in number from 73 to 82, with a mean of 78.2, males tending to have a few more than females. There are usually 13, sometimes 14, plates under the fourth toe.

PATTERN AND COLORATION: As far as known, *H. h. alvarezi* emerges from the egg with a pattern that closely resembles that of the juvenile of the nominate subspecies. However, the information as well as specimens available indicates that there is a steady increase in the amount of black at the expense of the lighter areas that occurs during the early years of life. Señor Miguel Alvarez del Toro,

who has supplied the majority of the preserved material, writes as follows: "I have closely watched the local *Heloderma* in our little zoo, where we have had several specimens alive, including one that we obtained eight years ago. . . . I have observed that the black form is spotted when young, but slowly, in the course of three years, it loses its spots; around the fourth year it becomes almost black."

Señor Alvarez's statement is borne out by the preserved specimens. The pattern is already virtually obsolescent on a preserved specimen (from El Sumidero near Tuxtla Gutiérrez), despite the fact that it has an over-all length of but 410 mm. The body is dark brown, with a few light brown rings on the vertebral ridge, and some bars similar in color on the flanks are discernible. Faint traces of the five light pairs of tail rings, most of them interrupted by black on the midline, are present on the dorsum. On the under side of the tail, however, the two pairs of light bands on the basal portion are well defined, pale yellow in color, and sharply set off from the dark brown ground color; the three distal pairs of rings are not so well defined. The venter is grayish brown, slightly paler than the dorsum, and faintly mottled with lighter gray.

The traces of the pattern discernible on this Chiapan specimen appear to represent the vestiges of markings not unlike those that are well defined on a slightly smaller specimen of *H. h. horridum* from Concepción, Oaxaca. On the other hand, an adult female with an over-all length of 545 mm. that was obtained at Rancho San Bartolo in Chiapas by Mr. Wendell Burger retains virtually as much of the pattern as the smaller specimen of *alvarezi* from El Sumidero. A few small clumps of light brown or dingy white are present on the dorsum of specimens from El Refugio near Cintalapa, and from El Gavilán near Ocozacoautla, individuals, respectively, 515 mm. and 635 mm. in total length. But the nearest approach to a completely uniform slaty-black coloration is to be seen on the largest specimen available, a male with an over-all length of 650 mm. that Mr. T. C. MacDougall obtained at Cintalapa in 1945.

It is still uncertain whether all adult specimens of *Heloderma* from the Atlantic drainage are so nearly devoid of pattern as the type and

paratypes. A higher percentage of such individuals may occur in some local populations than in others. Señor Alvarez informs us (*in litt.*) that he has never seen a spotted adult in the neighborhood of Tuxtla Gutiérrez: "I do not know how far to the north or east the black form ranges, but around Tuxtla Gutiérrez and along the Río de Chiapa [Río Grande or Río Grijalva on some maps] only the juveniles are spotted and the adults are uniformly black."

It may be added that the nearly black specimens of *H. h. horridum* that occasionally turn up in Guerrero, perhaps only from the vicinity of Chilpancingo, are large specimens. Those no larger than the average adult of *alvarezi* invariably possess a well-defined pattern, to judge from the limited material we have examined.

HABITAT

The Chiapan beaded lizard probably lives in the tropical deciduous forest, as inferred from the vegetation map of México (Leopold, 1950). Miranda (1952) indicates the region as being largely savanna, and all specimens thus far obtained are from the phytogeographic zone he maps as the Central Depression ("*Depresión Central*") of Chiapas. The savanna he maps is interspersed with deciduous forests, with pines and oaks on the higher hills. It may be doubted whether *alvarezi* occurs in the open, grassy savannas in the region, although it may occur in the gallery forests along the streams that flow through such areas, and probably it ranges into the lower limits of the pine-oak forest. Stuart (1954) has mapped the "sub-humid corridor" that probably corresponds most closely to the range of the race.

RANGE

At present *Heloderma horridum alvarezi* is known only from west central Chiapas, on the headwaters of the Río de Chiapa on the Atlantic drainage. It may be found farther eastward, and it is not impossible that the range extends into Guatemala.

LOCALITY RECORDS

Viquez (1935) reports a "*largetija venenosa*" in Costa Rica and crudely depicts a lizard resembling *Heloderma suspectum* and labeled "*Perro Sompopo*" (corrected to "*El Perro*

Zompopo" in a second edition of his work published ca. 1940). His discussion mentions the American species, "*el monstruo de Gila*," and other comments would lead the reader to infer that *Heloderma* is represented in Costa Rica. It seems probable that the native name, *perro zompopo*, refers to some other lizard erroneously assumed to be venomous. There is no evidence that *Heloderma* occurs even as far south as Honduras or Nicaragua.

Mr. J. T. Sackett informs us that specimens believed to be *Heloderma* have been found 18 miles north of Naranja, and possibly at La Unión in northern Guatemala. However, these records remain to be authenticated. Whereas statements of the range have frequently included "Central America," we know of no actual record for any specimen south of Chiapas. The type and paratypes, from the following localities, with approximate elevations given in parentheses, are the only specimens thus far available for study:

CHIAPAS

- Rancho San Bartolo (500–700 m.), U.I.M.N.H. No. 7029
- Cintalapa (545 m.), A.M.N.H. No. 65863
- El Refugio, near Cintalapa (600 m.), A.M.N.H. No. 70538
- El Gavilán, near Ocozacoaulta (650 m.), A.M.N.H. No. 70181
- Near Tuxtla Gutiérrez (550 m.), I.B.M., two specimens, type and paratype, not numbered
- El Sumidero, near Tuxtla Gutiérrez (550 m.), A.M.N.H. No. 70539

Heloderma suspectum suspectum Cope

RETICULATE GILA MONSTER

Plates 9 and 10

Heloderma horridum BAIRD (not of Wiegmann), 1859, Reptiles of the boundary, in United States and Mexican boundary survey, vol. 2, p. 11, pl. 26; lists "2971 Sierra de la Unión [=Sierra de Moreno on the boundary between the United States and México]. Sonora. A. Schott," figuring one specimen, now U.S.N.M. No. 2971a.

Heloderma suspectum COPE, 1869, Proc. Acad. Nat. Sci. Philadelphia, vol. 21, p. 5; (figure [26] in Baird's [1859] paper cited).

TYPE

By implication the specimen (U.S.N.M. No. 2971a) figured by Baird, whose paper and

figure are cited by Cope, may be considered the type. Two other specimens bearing the same number on tin tags now have the letters "b" and "c," respectively, added to the digits; these were collected at approximately the same time and at the same place as the type, although their existence is not indicated by either Baird or Cope. Under the circumstances it is questionable whether U.S.N.M. Nos. 2971b and 2971c can be considered cotypes, as authors have indicated.

The type was originally indicated as having been collected by A. Schott at "Sierra de la Unión. Sonora," now known to be in the vicinity of Monument No. 146, one of the markers on the International Boundary. Hence the type locality is the Sierra de Moreno, on the boundary between the United States and México. The locality can legitimately be listed either with localities in Sonora or in Pima County, Arizona.

DIAGNOSIS

At the specific level *H. suspectum* differs from *horridum* in having: (1) a tail that comprises no more than 55 per cent of the snout-to-vent length instead of 65 per cent or more; (2) a known maximum of 28 caudal vertebrae in contrast to 40; (3) fewer rows of subcaudal scales, 48 to 62 instead of 73 to 87; (4) a pair of enlarged preanal scales; (5) the splenial extended onto the inner surface of the coronoid (fig. 5); and (6) usually only one pair of infralabials in contact with the anterior chinshields. Also, *suspectum* has most of the upper surface of the head, except the snout, mottled with pink, unlike *horridum*, which nearly always has a uniformly black head, rarely with a few light scales near the occipital region. Aside from other differences, juveniles of *suspectum* have but four or five black bands on the tail, whereas juveniles of *horridum* possess six or seven. Also *suspectum* has one or two more maxillary teeth than *horridum* but lacks palatine teeth.

At the subspecific level *H. s. suspectum* differs from *H. s. cinctum* (to be described in a following section) in having a pattern that undergoes extensive changes during the ontogeny of the individual. Juveniles of the two races are not readily distinguishable, but *cinctum* retains most of the pattern characteristics of the hatch-

ling throughout its life. Adult specimens of *suspectum* are mottled or blotched with black and pink, with a higher percentage of black than of pink on the dorsum of individuals from most parts of the range. The lighter bands on the tail are mottled, blotched, or streaked with black, and the five (or four) black bands on the tail, including the black terminus, are either irregularly interrupted by rows of light scales or broadened at the expense of the lighter bands. In contrast the adult of *cinctum* retains the four distinct cross bands on the upper side of the trunk, each band containing a row of more or less round, pink or yellowish spots, usually three on each side of the midline (see pl. 11, fig. 1). Also the bands of the tail of *cinctum*, always five, are essentially like those of the juvenile, with well-defined black bands, solid in color, and about as broad as the intervening pink or yellowish bands, which rarely contain more than a few individual black scales.

By and large the scutellation of *suspectum* is essentially the same as that of *cinctum*, although the nominate subspecies generally has fewer rows of scales under the tail, the maximum for *suspectum* corresponding closely to the mean for *cinctum*, with statistically significant difference between the means. Also *suspectum* tends to have fewer internasals and superciliaries than *cinctum*, but these differences are minor. The tail of *suspectum* in proportion to the snout-to-vent length averages somewhat shorter than that of *cinctum*, a condition probably correlated with the fewer rows of subcaudals in the former.

NOTES ON THE TYPE

Although the type was never described, it has been depicted with fair accuracy by Baird (1859a) as far as the pattern, many features of the squamation, and the habitus are concerned. But the scales on the side of the head are not faithfully shown. Whereas the large scales anterior to the eye are in mutual contact, and those in the temporal region are separated by granular scales, Baird's figure would indicate that all the scales above the labials and lorilabials are widely separated by smooth skin. Figure 87 in Cope (1900), herewith reproduced as text figure 9, while somewhat diagrammatic, shows the characteristic scutellation

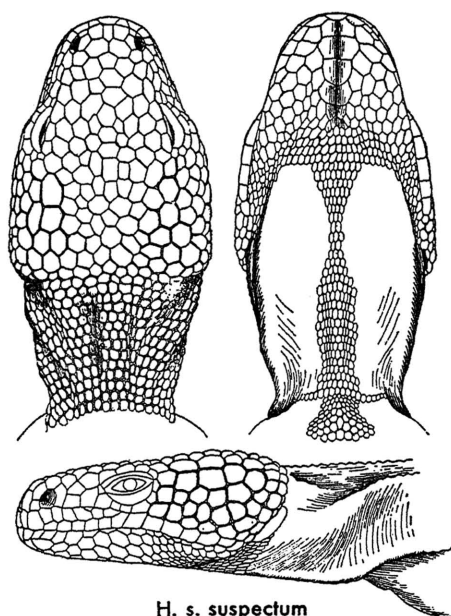


FIG. 9. Dorsal, ventral, and lateral views of the head of *Heloderma suspectum*, to show scutellation. Drawing from Cope, 1900. For names of individual scales, see plate 2.

of *suspectum* correctly for another Arizona specimen.

The type, now somewhat faded, but well preserved otherwise, is an adult female with an over-all length of 380 mm., the tail (125 mm.) comprising 49 per cent of the snout-to-vent length. The span of the outstretched fore limbs, excluding the claws, is 175 mm., for the hind limbs 172 mm. The claws on the hind feet are broken and incomplete, but the claw of the fourth finger measures 11.2 mm., the straight-line distance between the point and the dorsal insertion. The head is 34.6 mm. in width at the temporal region, 21.1 mm. at the level of the posterior superciliaries. The distance from the snout to the upper end of the ear opening is 43.7 mm.

The rostral is wider than high, and followed on the head by two postrostrals, the one on the right side being split horizontally, the upper portion being the larger, and in contact with one member of the pair of internasals, but separated from the rostral. There are three superciliaries and three canthals, the anterior one of which is in contact with the nasal, thus separating the supranasal from the postnasal.

There are two loreals, two preoculars, and three suboculars. Seven scales are present counted across the head between the posterior superciliaries; counting down the midline of the head there are 13 scales between internasals and the occiput, where granular scales surround the larger scales covering the osteoderms.

Thirteen supralabials, the second one reaching the nasal on the right but not on the left, are present on both sides of the head. There are six lorilabials on each side, in a single row on the right, but with the third scale wedged in above the second and fourth on the left. The infralabials are 15-15, of which only the first in each series reaches the anterior pair of enlarged chin-shields, which is followed by two additional pairs, with an enlarged scale on the right side behind the third pair that lacks a counterpart on the left. Contrary to Baird's figure, there are no more than 12 enlarged plates under any toe, and only 10 under the fourth toe.

On the under side of the body there are 70 rows of scales between the gular fold and the vent, 56 of which fall between the axilla and the groin. There are 55 transverse rows of scales on the tail posterior to the vent. Near the middle of the trunk 60 rows of scales can be counted around the body, and 30 in the first complete row at the base of the tail.

As mentioned above, the irregularly reticulated pattern of the trunk is accurately depicted by Baird. The type specimen, as have a high percentage of others obtained in the region centering around southwestern Pima County, has but four broad black bands on the tail, including the black terminus. The black band at the base of the tail is interrupted by lighter scales, whereas the distal three are virtually solid black, somewhat irregular at the edges, and considerably broader than the three intervening yellowish bands, which contain a few black scales, most of them in rows paralleling the wide bands. The limbs are mottled with the lighter color, now yellowish in the faded specimen, but probably pinkish in life.

MATERIAL EXAMINED

Of a total of 93 specimens (not including four skulls) of *H. s. suspectum* available for examination, 15 are from Sonora, two are from New Mexico, and the remainder are from

Arizona, the largest sample being that from Pima County. Those from Arizona are distributed by counties as follows: Yavapai, two; Gila, seven; Maricopa, nine, Pinal, three; Greenlee, three; Pima, 29; Graham, three; Santa Cruz, one; Cochise, three. Sixteen additional specimens have no locality data, or are accompanied by insufficient data for them to be allotted with certainty to any county. The sample is composed of 29 males, 41 females, and 11 juveniles the sex of which cannot be ascertained, even from an examination of the gonads. An additional 12 specimens include skins, heads, or eviscerated individuals of undetermined sex.

VARIATIONS IN THE SAMPLE SERIES

MORPHOLOGY: An analysis of ratios calculated for measurements discloses no significant differences between the male and the female, which cannot be distinguished by means of external characters. Were it possible to obtain measurements of the limbs and body of preserved specimens with absolute accuracy, slight mean differences might conceivably be demonstrated. We have found no important differences between the means for scale characters of the two sexes, and consequently the figures for the two have been combined in the description that follows.

The smallest specimen examined is a juvenile (U.S.N.M. No. 105218) taken in Gila County north of Globe; the specimen has an over-all length of 170 mm., snout-to-vent length, 120, the tail (50 mm.) comprising 42 per cent of the distance from the snout to vent. The largest specimen in the preserved series is a male (U.S.N.M. No. 61258) from Duncan, Greenlee County, Arizona. It is 520 mm. (nearly 20½ inches) from the snout to the tip of the tail; the tail is 171 mm. long, and comprises 48 per cent of the snout-to-vent length (349 mm.). The specimen is from a locality in the foothills on the periphery of the range. The largest females are two from Guadalupe Cañón in northeastern Sonora. Both specimens (U.S.N.M. Nos. 20097 and 20099) have over-all dimensions of 485 mm., but one has a snout-to-vent length of 325 and the other 315, with tails, respectively, 160 mm. and 170 mm. Woodson (1948) mentions a captive of unknown sex or origin that was 21.5 inches

long; it weighed "four pounds." Mr. Chas. A. Hewitt of Buena Park, California, who owned this specimen, informs us that on November 14, 1948, the specimen was 21¾ inches in length and weighed 4 pounds, 12 ounces.¹

It is not improbable that *H. s. suspectum* attains a somewhat greater maximum size than the largest specimen we have been able to examine. Ditmars (1907, p. 172) claims to have examined one with a total length of 24 inches (609 mm.), but this requires verification. Shufeldt (1887) says he has heard that a length of 26 inches is attained, but he adds that he has never seen "one anything like as big as that." Mauldin (1949) tells of a 24-inch specimen from an unidentified locality in Arizona, but his account is more intended to be humorous than factual, and the "measurement" is not to be taken seriously. Of 24 adult males examined, 33 per cent exceed 300 mm. in length; of 38 females, 29 per cent fall within the limits of 300 mm. and 327 mm. for the snout-to-vent length.

The ratio of the tail to snout-to-vent length varies from 0.41 to 0.52, averaging approximately 0.48 for both sexes, extremes for both also being approximately the same. Ratios for the head width (at eye level) to head length vary from 0.53 to 0.60, averaging 0.58, in males; in females the mean ratio is 0.57, with extremes of 0.54 to 0.61. The extremes of the same ratio for juveniles are 0.52 to 0.62, with a mean of 0.57. The head length comprises from 15 to 21 per cent of the snout-to-vent length, averaging approximately 18 per cent for both sexes. The distance between the toes of the outstretched hind limbs averages 69 per cent of the snout-to-vent length, with variations of 5 per cent above and below the mean that can be attributed in part to the difficulties involved in obtaining accurate measurements. The length of the claw of the fourth finger represents approximately 2 per cent of the snout-to-vent length, rarely as much as 3 per

¹ During the month of July, 1955, Mr. William Miller presented to the American Museum a live specimen measuring 21.5 inches in total length at the time it was captured on Mr. Miller's ranch, in Post Office Canyon, Peloncillo Mountains, Hidalgo County, New Mexico. Specimens of such dimensions have not been observed in Pima County, where the species is more frequently encountered. The larger individuals are virtually all from the eastern periphery of the range.

cent. The claws on the toes are perceptibly shorter, varying from 1.0 to 2.1 per cent of the snout-to-vent length. The claws of juveniles are somewhat longer than those of adults, possibly because they have not been subjected to appreciable wear.

SCUTELLATION: The rostral of *suspectum* is subject to considerable variation; possibly because of injury or abrasion it is often rough, or irregularly sutured, as though it were composed of smaller scales. Infrequently (in approximately 6% of the specimens) it is represented by three scales, with a median scale flanked by one on each side that may exceed the size of the one in the normal position, as depicted by Cope (1900, reproduced as our text fig. 9). But for their position, the lateral portions of the rostral are indistinguishable from the first supralabial, which normally falls below the prenasal. Usually there are two postrostrals, but three occur in 9 per cent of the sample. Similarly the internasals are normally paired, but three are present on 13 per cent of the heads examined.

The canthals are rarely in a straight row on the canthus rostralis, some falling on the border of the ridge. The canthals vary from one to four, but three are present in 91 per cent of the specimens, the first being wedged in above the nasal between the supranasal and the postnasal, without exception. Three superciliaries are usually present, but four are present in 17 per cent, and as many as five occur rarely. The number of scales between the posterior superciliaries on the top of the head varies from seven to eight, 65 per cent of the specimens having seven. There is greater variation in the number of scales between the internasals and the level of the ear aperture; counted as nearly as possible down the middle of the head these vary from 11 to 15, averaging 12.5.

The loreals vary in number from two to five, 41 per cent having two, 36 per cent having three, 22 per cent having four, with five occurring on but one side of a single individual. There are from four to nine lorilabials, averaging 5.7, sometimes in a single row, but not infrequently with some of the individual scales split. Two preoculars may be considered the normal number, although one is present in 23 per cent, and three occur in 4 per cent, of the specimens. There are from 10 to 14 suprala-

bials, with 12 as the mode as well as the mean; the second supralabial is in contact with the nasal in 82 per cent of the cases, separated from it by the anteriormost lorilabial in the remainder.

On the lower jaw there are from 12 to 16 infralabials, the mean being 14.3. Normally only one infralabial reaches the first pair of chin-shields, but two are in contact in 5 per cent. The mental is small and subtrapezoid, with a blunt apex extending between the first pair of chin-shields. Usually there are three pairs of enlarged chin-shields disposed along the mental groove, but four occur in 10 per cent of the specimens.

On the under side of the body there are from 62 to 72 (mean 66.0) scales between the gular fold and the vent, of which 48 to 59 fall between the axilla and the groin, with 52.9 as the average. Under the tail there are from 48 to 59 rows of scales posterior to the vent, with 52.8 as the mean. From 52 to 62 scales (mean 57.0) can be counted around the middle of the trunk, with from 26 to 31 in the first complete row encircling the tail, the mean being 27.9. There are from eight to 13 broad scales under the fourth toe, 11 occurring most frequently.

PATTERN AND COLORATION: Descriptions of the pattern entail consideration of the (1) ontogenetic changes, (2) individual variation within local populations, and finally (3) regional variations. The following notes, supplemented by plates 9, 10, and 12, summarize information in all three categories.

The ontogenetic changes in the pattern of *suspectum* have the same sort of trend discernible in *H. horridum*, with five dark areas on the dorsum of the neck and body that become obscured during the early years of life. The juvenile of *suspectum* emerges from the egg with a relatively simple pattern of sharply contrasting light (yellow or light orange) and dark (black or nearly so); as a result of changes in the color of individual scales, light areas appear within the original dark ones and *vice versa*. The snout, the sides of the head, and the entire gular region of the hatchling are black, the color extending posteriorly across the ear aperture on the sides and onto the neck below. From the eye level posteriorly, the upper surface of the head is pinkish or yellow, with dark spots or curved streaks on each side of the midline

that form a pattern roughly bilaterally symmetrical. Occasionally a few pale scales are present on the middle of the head anterior to the eye level.

The upper surface of the neck is patterned with a black reticulum confluent with the black on the under side. This reticulated area on the neck may or may not be connected with the first of five "saddles," or what are essentially irregular, double, black bands encircling the body. Occasionally one band is connected to an adjacent one on the body, and each band encloses from four (at the groin) to as many as nine light spots, usually four on each side of the body, with the lowermost pair falling on the belly. A pale area extends across the sacrum onto the thighs, followed posteriorly by a black band that encircles the base of the tail. Including the latter, as well as the black terminus, there are from four to five black bands alternating with three or four yellow or pinkish bands on the tail. The black bands tend to be wider than the light bands, and if there are but four of the former, they are considerably wider than the light bands. The limbs are black except for the proximal half of the upper (humeral and femoral) segment; a black line extends backward along each side of the chest from the dark area on the under side of the neck to the under side of each fore limb, reaching the black of the fore limbs. Similarly, the black of the hind limbs may be confluent with a black patch in the preanal region, with the first black band on the tail, or with both.

During the early years of life, quite possibly during the second and third summers, scales that were black in the hatchling change in color to yellow or pink so that the upper surface of the snout, and areas on the limbs, become mottled or streaked with light scales. On the majority of individuals (but rarely on individuals from Sonora or southwestern Pima County, Arizona), lighter scales, often in rows or clumps, make their appearance in the black bands on the dorsum and on the tail. Usually the black bands on the tail become wider at the expense of the light bands. At the same time, or approximately so, black dots or small blotches appear in the paler areas that separated the bands or saddles on the body, where the pale areas are also invaded by extensions of black from the cross bands so that the bands

become obscured in the resulting reticulum.

Juveniles representing several portions of the range are available, and all have much the same sort of pattern. However, the changes in pattern that accompany growth differ in various local populations. Although no two adult Gila monsters have identical patterns, there is one sort of pattern that characterizes the majority of individuals from any given area, with relatively few departures from the mode. Most specimens from northeastern Sonora (pl. 12, fig. 5) have the black reticulum consisting largely of broad lines containing few light scales, whereas on specimens from the area around Tucson in southeastern Arizona, rows of individual light scales within the black of the reticulum are ordinarily present.

Many individuals from southwestern Pima County (see pl. 17) and probably from adjacent northwestern Sonora retain the black limbs and seemingly most of the black of the juvenile, with extensive increases in the amount of black on most areas of the body and little if any increase in the paler elements of the pattern. The net result is a pattern composed of highly irregular blotches and spots on a black ground color. These are among the darkest of all *H. s. suspectum* examined, although an occasional dark individual is known from the vicinity of Tucson. One from the Kelly Ranch (pl. 12, fig. 4) north of that city is extremely dark, with most of the light scales on the dorsum in small clumps or in rows of individual scales.

Only one adult specimen (pl. 9, fig. 3) from New Mexico has been available for examination, and, if this is representative, the easternmost population seems to be characterized by having a somewhat more mottled pattern than most specimens from the vicinity of Tucson.

At the other extreme are the pale specimens from the northern edge of the range of the nominate subspecies, particularly in the foothills of Gila and Yavapai counties, and from the vicinity of Phoenix, in Maricopa County. Specimens from this region are essentially intermediate between *suspectum* to the south and *cinctum* to the north and west. On the basis of scale characters as well as their pattern these individuals might well be termed intergrades. Vestiges of the complex double black bands of the juvenile are still discernible, although black blotches appearing between them tend to con-

nect adjacent bands, and rows of light scales have invaded the black bands on the tail. But in having only a few isolated black spots, rather than rows of dark scales, in the light tail bands, the specimens are not dissimilar from *cinctum*.

A large specimen from 3 miles south of Aguila (F. A. S. No. 2990, pl. 12, fig. 6) in the northwestern corner of Maricopa County is interpreted as an intergrade between *suspectum* and *cinctum*, even though it occurs west of specimens from near Wickenburg that have been called *cinctum*. Despite the fact that the black bands on the body and tail are clearly evident, the black spots between the bands are more numerous than in typical *cinctum*. The uniformly black bands on the tail have been retained, but the white bands separating them are more liberally sprinkled with black scales than is characteristic of specimens from Utah and Nevada. Actually the pattern is rather unusual for the species, so that the specimen could be considered an atypical *cinctum*. However, a number of *suspectum* characters are present and the specimen is so manifestly intermediate in pattern characters that we list it under *suspectum* with the explanation that it shows intergrading tendencies.

To recapitulate, there is a fair amount of variation in the adults of local populations, with an occasional dark specimen being found as far north as eastern Pima County. Nevertheless, a general trend is discernible, with the majority of the darker specimens originating in western Pima County and presumably the adjacent portion of northwestern Sonora. The population from central and northeastern Sonora is characterized by having a bold, black reticulum, with little invasion of the black by lighter scales, such as occurs in specimens from southeastern Arizona, where the majority of specimens have a mottled reticulum.

Towards the northern extremity of the range dark individuals seemingly do not occur. There is a general tendency towards retention of the principal elements of the juvenile pattern, many individuals having a pattern approaching that of *cinctum*, but with more mottling of the tail bands and less discrete black saddles or cross bars than normally occur in the northern subspecies. But for the dark population in western Pima County, the general picture is that of a cline, with a south-to-north trend towards in-

creasing paleness. However, this statement alone would represent an oversimplification of what is actually a complex situation.

It may be added that only 50.0 per cent of the specimens from Sonora, and 44.0 per cent of those from Pima County, Arizona, have five black tail bands, while the majority of specimens, 76.0 per cent of the sample representing Yavapai, Maricopa, Gila, Graham, Greenlee, and Cochise counties in Arizona and Hidalgo County in New Mexico, have five black tail bands.

HABITAT

In Arizona the Gila monster is primarily an inhabitant of semi-arid, rocky regions, more especially near or in the foothills of the mountains (pl. 14, fig. 1). Ruthven (1907) comments on the lack of published information concerning the habitat and was the first to report that "About Tucson [in Pima County, Arizona] we found that its principal habitat was alluvial slopes at the foot of the Santa Catalina Mountains (Sahuaro-Ocotillo association), where it is quite common. In four weeks collecting none were seen by us on the plains of this region, and Prof. Thorner informed us that specimens were rarely secured in this habitat." Van Denburgh and Slevin (1913) note that specimens taken in the vicinity of Tucson, Arizona, were found in association with giant cactus (*Cereus gigantea*) and creosote bush (*Larrea tridentata*), as well as in the oak belt. Dr. A. I. Ortenburger, in field notes (on file in the American Museum of Natural History) made during the summer of 1923, records one specimen from the foothills of the same mountains that was taken in the mesquite (*Prosopis*) association 14 miles north of Tucson, another in cholla (*Opuntia*) and yucca, while a third was taken in a similar association near a paloverde tree (*Parkinsonia*).

King (1932) states that *H. s. suspectum* is common in the foothills of the Santa Catalinas near Tucson and that he also found it in the foothills of the Santa Rita Mountains. Gloyd (1937) reports finding *suspectum* "in the Mesquite plain of the San Pedro Valley, and on the desert floor near the foothills of the Santa Catalina Mountains; another on a rocky ridge in the desert, and a fourth in a sandy arroyo." Kauffeld (1943) reports that two specimens

taken in Bear Canyon in the foothills of the Santa Catalina Mountains northeast of Tucson were found together "in a clump of vegetation in the dry, rocky stream bed," commenting further that "Although the stream bed was dry, for the most part, where the above specimens were collected there were, nevertheless, well-filled water pockets in the rocks."

The moisture requirements of *H. s. suspectum* are discussed in a succeeding section of the present paper. Here it is pertinent to note that the species does not inhabit "arid, barren" regions as sometimes stated (H. M. Smith, 1935, p. 145) or implied. In fact the evidence available indicates that the Gila monster rarely if ever occurs in the relatively open flats largely restricted to creosote bush. This sort of growth usually indicates the presence of a very shallow soil underlain by an impervious caliche, according to Nichol (1937), and such areas are avoided by many animals, possibly because burrows are difficult to construct or to maintain during periods of heavy rain. Places where reptiles can find suitable shelter are, therefore, not abundant.

It may be inferred from Nichol's useful map of the natural vegetation of Arizona that *Heterodermus* is more abundant in, but not restricted to, areas of "the southern desert occupied by the palo verde-cacti type of desert." Such deserts are by no means barren. There are many variations in the structure of desert floras, but several species of cactus and woody plants are present, as well as specialized desert grasses and vines that are able to withstand prolonged periods when no water is available.

The mean annual rainfall for Tucson, near the center of the range of *H. s. suspectum*, is 11.5 inches but subject to considerable fluctuation from year to year. During 30 consecutive years a minimum of 5.1 inches was recorded for one year, whereas 24.1 inches was recorded for the maximum year of the period. During nine of the 30 years the rainfall was 25 per cent, or more, below the average. Thus *suspectum* inhabits a region subject to periodic droughts, which, it may be assumed, the majority of individuals survive. It is possibly significant that all the desert regions inhabited by *suspectum* characteristically have heavier rains during the warm season of summer than during the cold winter months. For the period from

1875 to 1927, according to Nichol (1937) the average rainfall at Tucson for the summer months of June, July, and August was 5.7 inches, with scarcely more than half of the rainfall (5.8 inches) occurring during the remainder of the year. Thus the maximum rainfall occurs during the warm months when thermal conditions do not inhibit the activities of the Gila monster.

The absence of *suspectum* west of the Organ Pipe National Monument in southwestern Pima County, and its failure to penetrate (or possibly to survive in?) the deserts of California can probably be attributed to the paucity of summer rainfall in the regions bordering the lower portions of the Colorado River. The map (United States Department of Agriculture, 1941, p. 712) showing the average warm-season precipitation from April to September in the United States from 1899 to 1938 shows clearly that from 5 to 10 inches of summer rainfall characterize most of the region inhabited by *suspectum*, with the line marking the 2-inch level corresponding closely to the western limit of the range of the species.

As far as the altitudinal distribution is concerned, the majority of the localities from which the Gila monster has been recorded in Arizona fall between the elevations of 2500 and 4000 feet. There appears to be no reason to doubt the authenticity of locality data for a specimen said to have been taken at Old Gila Bend, which lies at an approximate elevation of 736 feet. It is manifest that the species is absent from the higher mountains and plateaus in Arizona, but several records from the southeastern corner of the state show conclusively that altitudes approximating 5000 feet are attained. It is possible that similar elevations approaching 5000 feet are inhabited by the species in Yavapai County, where a specimen presumed to resemble specimens showing intergrading tendencies has been reported. However, this record, for Humboldt, requires verification.

In New Mexico, at the eastern periphery of the range, *H. s. suspectum* evidently occupies habitats similar to those in which it lives in Arizona. Koster (1951) has summarized the information for New Mexico, including authenticated records, as well as some that require verification, and others that assuredly repre-

sent escaped individuals transported beyond the limits of the natural range, as Koster himself notes. One individual reported by Koster was taken on the lower southwest slope of Cienega Peak at an approximate elevation of 4000 feet in Hidalgo County near the Arizona border. The region is described as being one of the "general desert grassland vegetation type which, because of slope and exposure, leaned strongly toward the yucca-cactus association. The dominant plants in the vicinity of the point of capture were, in the order of decreasing abundance, creosote bush (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), and palmilla (*Yucca elata*)."

Specimens from the McGee mine in the Philadelphia Zoological Garden are described by Koster as being from "an elevation of approximately 4500 feet in a volcanic region where the dominant vegetation consists of two types of yuccas." Redrock, near the point of capture of specimens also sent to Philadelphia, lies at an elevation of 3900 feet on the headwaters of the Gila River in Grant County. Koster describes the region as "one of desert grasslands with local stands of palmilla, mesquite (*Prosopis juliflora*) and creosote bush, with dwarf oaks in some of the draws."

Durham (1951) states that a specimen taken north of Hermosillo in Sonora was in an environment characterized as "relatively level terrain sparsely covered with chaparral and scrubby trees characteristic of the Upper Sonoran Life Zone." The vegetation north of Hermosillo is not aptly termed "chaparral"; it is mapped as "mesquite-grassland" by Leopold (1950). Farther south in Sonora, to the northwest of Guaymas, Taylor (1938a) mentions that three individuals were "captured in the sand near the point of meeting of the sandy beach and the scrub." Another was "found on the top of the low mountain rising from the edge of the sea."

When the information presented above is summarized, it is evident that the *H. s. suspectum* is largely restricted to the Lower Sonoran Life Zone, although it occurs above this zone in the oak belt (usually considered as Upper Sonoran), more often in rocky situations with moderate amounts of vegetation. Habitats range in elevation from near sea level to a maximum approximating 5000 feet in re-

gions subject to periodic droughts but having an average warm-season precipitation of from 2 to 10 or more inches.

RANGE

The reticulate Gila monster, *H. s. suspectum*, is known to occur from near Guaymas on the coast of the Mexican State of Sonora northward and westward to Yavapai County in central Arizona; here the limit of the range extends southeastward along the edge of the Central Plateau into Grant and Hidalgo counties in extreme southwestern New Mexico. Specimens from northwestern Maricopa County and those from Yavapai and Gila counties in Arizona possess characters indicating intergradation with *H. s. cinctum*, the range of which lies to the west and north. Intergradation with *cinctum* may possibly occur in eastern Yuma County, but specimens from the area are lacking. Records for Luna and Dona Ana counties east of the authenticated periphery of the range in New Mexico require verification.

Heloderma s. suspectum is largely restricted to the eastern portion of the "Sonoran Biotic Province," as mapped and defined by Dice (1943), but the range also encompasses the northern portion of the "Apachian Province," which, as noted by Bogert and Oliver (1945, p. 337), represents little more than a region where the ranges of plains elements interdigitate with those of species inhabiting the mountains. Similarly, the boundaries of faunal areas in southern Arizona mapped by Gloyd (1937) have little bearing on interpretations of the distribution of *Heloderma* in Arizona. For the most part the range of *H. s. suspectum* falls within the limits of the Sonoran Desert, as mapped by Shreve (1942), except that the lizard occurs considerably farther eastward in northeastern Sonora and southeastern Arizona than Shreve is willing to extend the desert.

LOCALITY RECORDS

The list of localities that follows includes (1) those for specimens examined, which are listed by museum number, (2) records from the literature or from correspondents with the source indicated, and (3) a few for live specimens, all those listed having been examined. Localities based on sight records are included in the list preceded by a question mark (also

on map 2 in similar fashion); such records are always open to some doubt, and several certainly require verification on the basis of actual specimens. We do not include records for California, which, as Woodson (1949c) who reviewed the literature concerning such records points out, are based on supposition, escaped individuals, or misidentifications. As early as 1869 Cooper commented on the absence of *Heloderma* in California. Vorhies (1917, p. 367) and Klauber (1945a, p. 152) note that the banded gecko, *Coleonyx variegatus*, is often mistaken for a young Gila monster. Similarly, we consider such extralimital records as that of English (1927) for Texas to have resulted from the escape of transported captives. Vorhies (1928) has already commented on such "artificial extensions of range," as Gila monsters, and other animals easily captured, are frequently transported by motorists and lost en route. Yarrow's (1875) early record for a lizard "presumably of this species" at San Ildefonso, New Mexico, is unlikely to be confirmed. Altini's (1942) record for "Mata-moros," México, is certainly in error, as are numerous others in the same report. Shannon (1954a) mentions records from Ehrenberg and Parker, in Yuma County, Arizona, that he considers doubtful. They could be authentic, but verification is desirable. To judge by the few specimens from the western periphery of the range, they would be referable to *H. s. cinctum* rather than to *H. s. suspectum*. Examination of such specimens would provide clues to the authenticity of the localities.

Specimens listed from localities preceded by an asterisk (*) are intermediate between *suspectum* and *cinctum* in characters of the pattern and scutellation. Such specimens are essentially intergrades, but, because they represent the northern extreme of a general south-to-north trend (or a cline of sorts) in the characters of *H. s. suspectum* as a whole, we prefer to list them (including some reported by others and not examined by us) as specimens of *suspectum* that bear closer resemblances to the race inhabiting the region to the north and west than do specimens from the southern portions of the range.

Approximate elevations are given whenever possible (in parentheses), although it is realized that in many instances collectors have given

the town or city nearest the actual point of capture as the source of individual specimens. A place only a mile away in airline distance may easily be several hundred feet above or below the locality on the label of specimens from mountainous portions of the range. When the higher mountain ranges, without qualifying statements, are given by collectors as the source, we have assumed that the specimens actually came from the foothills, as indicated in brackets. Elevations and distances are given in feet or miles for localities in the United States, whereas for those in México the metric system is used, following the customs of the respective countries.

UNITED STATES

ARIZONA

Yavapai County

- *Fort Verde (3000 ft.), A.M.N.H. No. 7246 (stuffed)
- *Kirkland (3927 ft.), M.V.Z. No. 9189
- ?*Humboldt (4900 ft.), Woodson, *in litt.*

Maricopa County

- *3 miles south of Aguila (2200 ft.), F.A.S. No. 2990
- *"5 miles from Marinette" (1150 ft.), S.D.S.N.H. No. 17596
- *Cave Creek (2300 ft.), Van Denburgh and Slevin, 1913, p. 407
- *Phoenix (1100 ft.), A.M.N.H. No. 8728, U.S.N.M. Nos. 44678, 56787
- *Paradise Valley (1300 ft.), Van Denburgh and Slevin, 1913, p. 407
- *Tempe (1175 ft.), U.S.N.M. No. 15942
- *"Near Mesa?" (1250 ft.), L.M.K. Nos. 25861, 25862
- *Old Gila Bend (736 ft.), U.S.N.M. No. 29371

Gila County

- *Roosevelt Dam (2250 ft.), Van Denburgh, 1922, p. 473
- *Roosevelt Lake (2150 ft.), U.S.N.M. No. 54446
- *Salt River at east end of Roosevelt Lake (2150 ft.), C.N.H.M. No. 26141
- *"Roosevelt Lake Area" (2150 ft.), Little, 1940, p. 263
- *Tonto National Monument (2150 ft.), Arnberger, 1948, p. 209
- *8 miles north of Miami (3400 ft.), U.M.M.Z. No. 84938
- *"Globe-Young Road," U.S.N.M. No. 1052218
- *Globe (3544 ft.), U.S.N.M. No. 46320, C.N.H.M. No. 15096

UNITED STATES

Gila County

- *Rice, Van Denburgh, 1922, p. 473
- *San Carlos (2532 ft.), N.S.N.M. No. 17087

Pinal County

- Casa Grande (1390 ft.), Van Denburgh, 1922, p. 473
- Picacho (1616 ft.), S.D.S.N.H. No. 17124
- 7 miles northwest of Owlhead, L.M.K. No. 27175
- 9 miles north of Oracle Junction (3000 ft.), L.M.K. No. 29449

Pima County

- Near Sawtooth Mt. (3000 ft.), C.M. No. 4448
- 12 miles northwest of Tucson, on Casa Grande Road (2000 ft.), A.M.N.H. No. 26083
- 22 miles north of Tucson (3000 ft.), A.M.N.H. No. 26080
- Western foothills of Santa Catalina Mts., 21 miles north of Tucson (3000 ft.), Gloyd, 1937, p. 114
- Cañada del Oro, near foothills of Santa Catalina Mts. (2800 ft.), A.M.N.H. No. 66998 (skeleton)
- West side of Cañada del Oro, 18 miles north of Tucson (2800 ft.), Gloyd, 1937, p. 114
- [Pusch's] Steam Pump, about 18 miles north of Tucson (2600 ft.), Van Denburgh, 1922, p. 473
- 1.5 miles south of Pusch's Steam Pump (3100 ft.), A.M.N.H. No. 26084
- 3 miles east of Pusch's Steam Pump (3100 ft.), A.M.N.H. No. 26076
- Kelly Ranch (2800 ft.), U.M.M.Z. Nos. 69979, 69980
- Ventana Canyon, Santa Catalina Mts. (2700 ft.), Van Denburgh, 1922, p. 473
- Bear Canyon, northeast of Tucson (3100 ft.), A.M.N.H. Nos. 63785, 63786
- "Foot Hills Station" [not located], Santa Catalina Mts., S.U.M. No. 10047 (skull)
- Near Oracle Road, 14 miles north of Tucson (3100 ft.), A.M.N.H. No. 26078
- Near Oracle Road, 10 miles north of Tucson (3000 ft.), A.M.N.H. No. 26077
- "On Oracle Road, n. of Tucson" (3000 ft.), C.M. No. 4447
- 6 miles north of Tucson, in foothills of Santa Catalina Mts., A.M.N.H. No. 26081
- Fort Lowell, S.U.M. Nos. 1964, 1956, 1967, 1968, 2576, 2577
- "Near Tucson" (2400 ft.), L.M.K. Nos. 22875, 29227, C.M. No. 21318

UNITED STATES

Pima County

- Tucson (2400 ft.), S.D.S.N.H. No. 13915, A.M.N.H. No. 62518
- 3.5 miles west of Tanque Verde (2700 ft.), A.M.N.H. No. 62707
- Tanque Verde Ranch, west of Tanque Verde Mts. (2700 ft.), S.D.S.N.H. No. 13914
- Converse Ranch, western foothills of Tanque Verde Mts. (2700 ft.), S.D.S.N.H. No. 12151
- Xavier (2600 ft.), L.M.K. No. 32531
- Escuela (2400 ft.), L.M.K. No. 32336
- 10 miles south of Tucson, near Xavier (2600 ft.), C.M. No. 19338
- 21.5 miles southwest of Tucson on Ajo Road (2450 ft.), L.M.K. No. 41166
- 23 miles southwest of Tucson on Ajo Road (2450 ft.), L.M.K. No. 40960
- [Foothills of] Santa Rita Mts., 7 miles northwest of Madera Canyon (4000 ft.), C.M. No. 19348
- Quijotoa, A.M.N.H. (alive)
- Gray's Ranch, Organ Pipe National Monument, S.D.S.N.H. No. 17875
- "10 miles [west-north-] w. of Sonoyta," Hensley, 1949, p. 152
- "Pima County" A.M.N.H. Nos. 27190, 27200

Santa Cruz County

- Foothills of Santa Rita Mts., [ca] 50 miles southeast of Tucson (4000 ft.), U.S.N.M. No. 118598 (head only)
- 1 mile southwest of Patagonia, Sonoita Creek (4000 ft.), C.M. No. 25220

Graham County

- [Foothills of] Graham Mts., U.S.N.M. No. 51526
- [Foothills of] Mt. Turnbull, Yarrow, 1875, p. 563 (now U.S.N.M. No. 8454, erroneously catalogued as being from "Mt. Trumbull")
- Fort Grant Road, 8 miles southwest of junction with U. S. Highway 70, F.A.S. No. 288
- Safford (2900 ft.), Van Denburgh, 1922, p. 473
- 10 miles south of Safford, N.S.N.M. No. 51732

Cochise County

- Cave Creek (4600 ft.), Van Denburgh, 1922, p. 473
- Camp J. A. Rucker, U.S.N.M. No. 10686
- Sulphur Springs Valley near Gleason (4923 ft.), C.M. No. 6649
- McNeal (4200 ft.), (alive)

UNITED STATES

Cochise County

- San Pedro Valley, 10 miles northeast of Fort Huachuca (4200 ft.), Gloyd, 1937, p. 114
 Foothills of Mule Mts., near Don Luis (5000 ft.), Gloyd, 1937, p. 114
 Near Naco (4550 ft.), L.M.K. No. 40961
 Ramsey Canyon, Huachuca Mts. (5000 ft.), Van Denburgh, 1922, p. 473
 "Dunlap's Ranch" (not located), U.S.N.M. No. 46321

Greenlee County

- Duncan (3642 ft.), U.S.N.M. Nos. 62573, 68062, 61258

NEW MEXICO

Hidalgo County

- Virden, Koster, 1951, p. 100
 15 miles northwest of Lordsburg, Philadelphia Zoological Garden (alive)
 "West of Lordsburg" (4245 ft.), Shaw, 1950, p. 38
 "Sent from Lordsburg," U.S.N.M. No. 39049
 6 miles southwest of Steins, Shaw, 1950, p. 38
 Lower southwest slope of Cienega Peak (4000+ ft.), Koster, 1951, p. 97
 Near McGee Mine, Peloncillo Mts., 21 miles southwest of Lordsburg (4500 ft.), Philadelphia Zoological Garden (alive)
 Miller Ranch, Post Office Canyon, Peloncillo Mts. (live specimen received too late to map)

Grant County

- ?Silver City (5931 ft.), Shaw, 1950, p. 38
 L. C. Canyon, 4 miles northwest of Redrock, Koster, 1951, p. 100
 Redrock (3900 ft.), Shaw, 1950, p. 38
 One-half mile east of Redrock (3900 ft.), Koster, 1951, p. 98

?Luna County

- ?16 miles east of Deming, Koster, 1951, p. 101

?Dona Ana County

- ?Aden Crater, 16 miles southwest of Afton, Koster, 1951, p. 100

MÉXICO

SONORA

- [Near Pozo Cipriano], Hensley, 1949, p. 152
 Sierra de Moreno, Monument No. 146 on International Boundary (1000 m.), U.S.N.M. Nos. 2971a (type), 2971b, 2971c

MÉXICO

Sonora

- Cañon de Guadalupe (1000 m.), U.S.N.M. Nos. 20997, 20998, 20999
 San Bernardino (1000 m.), U.S.N.M. No. 20996
 "Niggerhead Mountain" [=Cerro de Gallardo, southeast of Monument No. 82 on International Boundary] (1000 m.), U.S.N.M. No. 20995
 Near Monument No. 88 [on International Boundary] (1000 m.), U.S.N.M. No. 2100
 19 miles north of Bavispe (1000 m.), S.U.M. No. 12916
 7 miles northwest of Magdalena (750 m.), L.M.K. No. 40033
 5 miles south of Imuris (790 m.) S.D.S.N.H. No. 18191
 3.2 miles west of Trincheras (820 m.), M.V.Z. No. 28928
 Llano (700 m.), S.U.M. No. 12915
 10 miles south of Noria (700 m.), U.M.M.Z. No. 72233
 "Nearing Hermosillo" (211 m.), Durham, 1951, p. 460
 [Punta] San Pedro (0+ m.), Cope, 1900, p. 483
 Near La Posa, 10 miles northwest of Guaymas (0+ m.), Taylor, 1938a, p. 484
 "Between Yavaros and Agiabampo," F.A.S. No. 8073 (received too late to map)

[CHIHUAHUA]

[There are no definite records for Chihauhau, but Mr. Alden Hayes (*in litt.*, April, 1955) recalls seeing a Gila monster north and somewhat to the west of Casas Grandes, on the drainage of Lago Guzman. Further collecting in the region may substantiate the record.]

Heloderma suspectum cinctum,
 new subspecies

BANDED GILA MONSTER

Plate 11

Heloderma horridum, COPE (not of Wiegmann), 1866, Proc. Acad. Nat. Sci. Philadelphia, vol. 18, p. 303; specimen from "Fort Whipple," actually from La Paz, Yuma County, Arizona.

Heloderma suspectum MERRIAM, 1893, in Stejneger, North Amer. Fauna, no. 7, pt. 2, p. 194; specimen from 8 miles below Bunkerville, in Clark County, Nevada, mentioned. WOODBURY, 1931, Bull. Univ. Utah, vol. 21, no. 5, p. 52; records specimens from Santa Clara Valley and St. George, Washington County, Utah.

TYPE

Number 7456, an adult male, in the collection of the American Museum of Natural History, collected by Mr. William H. Rogers, at Las Vegas, Clark County, Nevada, April 28, 1919. Las Vegas is located in the Mojave Desert at an elevation of 2033 feet in the Las Vegas Valley, which drains eastward into the Colorado River. Since the completion of Hoover Dam, the drainage from the valley is directly into the body of water known as Lake Mead.

DIAGNOSIS

This subspecies differs from the nominate race (as well as from all races of *H. horridum*) in that the adult retains virtually all elements of the juvenile pattern, which undergoes only minor modifications during the post-natal ontogeny. The four black "saddles" or irregular, double cross bands (see pl. 11, figs. 1-3) containing lighter spots present on the upper surface of the trunk of the hatchling are readily discernible in the adult, in contrast to *H. s. suspectum*, the adults of which have a reticulate pattern, with the cross bands nearly or completely obscured. Similarly the adult pattern on the tail of *suspectum* consists of four or five black or dark brown bands (including the terminus), which are either heavily mottled with pink or yellow or considerably broader than the three or four intervening light bands, which are heavily mottled with black. In contrast the tail (see fig. 15) of the adult in *cinctum* is invariably patterned with five black or dark brown bands that alternate with four yellow or pinkish bands, with relatively little if any mottling in either, and with the dark bands approximately as broad as the contiguous light bands. On the whole, *cinctum* tends to be paler than *suspectum* in the adult stage.

Juveniles of the two subspecies are indistinguishable in pattern characters. Adults of *cinctum* are readily distinguished from those of *suspectum* on the basis of pattern characters, although some confusion with intergrades between two races may be anticipated.

DESCRIPTION OF THE TYPE

An adult male, with an over-all length of 483 mm., a snout-vent length of 315 mm., with the tail length (168 mm.) comprising 53 per cent of the distance between the snout and the vent. The distance between the tips of the long-

est toes (excluding the claws) when the hind legs are outstretched is 220 mm.; for outstretched fore limbs, 223 mm. The ratio of the hind-leg span to the snout-vent length is 0.73. The claw on the fourth toe of the hind limb is 5.4 mm. in length; the claw of the corresponding digit of the fore limb is slightly longer but appears to have been subjected to somewhat more wear.

The head is widest at the temporal region, where the diameter is 52.4 mm., narrower anteriorly, with a diameter of 29.5 mm. at eye level. The distance between the snout and the gular fold is 89 mm. The head length, measured from the snout to the anterior border of the ear, is 56.4 mm., or 18 per cent of the snout-to-vent length. The ratio of the head width (at eye level) to head length is 0.52.

A large rostral, broader than high, extends to a blunt apex at the lower end of the suture between two large postrostrals, with a small median scale above the suture. As the latter scale does not reach the rostral, it is included in the count for the internasals, the normal pair of which meet on a common suture behind the median scale. The supranasal is separated from the postnasal by the first canthal. There are two loreals on each side, with four canthals on the right (one below the ridge which might be construed as a loreal but for the fact that the upper end separates two canthals) side, three on the other. Encircling the eye on each side are two preoculars, three superciliaries, three postoculars, and two suboculars. There are 11 supralabials on the right, 13 on the left. Fourteen infralabials are present on each side, the first in broad contact with the anteriormost of three pairs of enlarged chin-shields. The mental is slightly wider than high, with tapering sides, terminating posteriorly in a blunt apex at the common suture of the first pair of chin-shields. The gular scales are like those of other members of the genus.

There are 71 rows of flattened ventrals between the gular fold and the vent, 55 of which fall between the axilla and the groin. Fifty-six rows of scales encircle the body halfway between the axilla and the groin. On the under side of the tail there are 60 transverse rows of scales, with 31 counted around the first regular row behind the vent. Thirteen enlarged plates or lamellae are present on the under side of the fourth toe of both hind limbs.

The pattern on the dorsum is shown in figure 1 of plate 11. The snout is uniformly dark brown, probably black or nearly so in life, with the color extending posteriorly to the eye level on the top of the head and on the sides of the head through the temporal region beyond the ear aperture. Behind the ear opening on each side the darker color is confluent with a coarse reticulum that extends over the neck and onto the body, with a somewhat ovate dark spot on the right side that is separated from the reticulum. An irregular dark blotch is present in the axillary region on each side. On the trunk there are four irregular double cross bands or "saddles," the anterior three of which enclose from five to seven somewhat rounded or elongate light areas that are from three to five scale rows in width. A few isolated scales or rows of scales are present in the darker areas of the complex cross bars, and a few isolated patches of dark scales are present in the lighter areas between. But on the dorsum and sides none of the saddles is actually confluent with an adjacent one. Examined from below it may be seen that the cross bars actually encircle the body, becoming narrower on the belly, where the pattern tends to follow the rows of flattened, squarish scales, and includes lighter bars rather than the rounded areas like those of the bands on the dorsum. Also the posteriormost band is confluent with the preceding one on the right side of the median line of the belly.

The entire throat and gular region is dark, with one or two faintly lighter scales. The upper portion of the limbs is yellowish, with the lower portion dark but mottled with yellowish scales. A light area interrupted by a small dark blotch on each side is present above the sacral region. On the tail there are four dark bands alternating with four light bands, followed by a black terminus (counted as the fifth band in tabulations as well as in keys). The dark bands encircle the tail, tending to be broader on the dorsal surface than on the ventral surface where the first or proximal band extends forward as a Y-shaped area behind the vent.

MATERIAL EXAMINED

In addition to the type, 26 specimens (paratypes) referable to *cinctum* have been available. The sample includes 16 males and six females; the sex of the remaining five specimens could not be ascertained because three are

juveniles, one specimen is too badly preserved, and another consists of the head only. The type is the only specimen from Nevada now available; Utah is represented by 11 specimens, all from Washington County. Arizona is represented by one specimen from Mohave County, one from Yuma County, three from Yavapai County, and 10 specimens from Maricopa County.

VARIATION IN THE SAMPLE SERIES

MORPHOLOGY: The smallest specimen in the series (from 0.5 mile west of Wickenburg in Maricopa County, Arizona, F.A.S. No. 2996) has an over-all length of 193 mm., with the tail (60 mm.) comprising 45 per cent of the snout-to-vent length (133 mm.). Post-juveniles, one from near Wickenburg (F.A.S., no number), and one from Bloomington, Utah (L.M.K. No. 25599), are, respectively, 227 and 241 mm. in over-all length, with the tail comprising 52 and 49 per cent of the snout-to-vent length.

The largest specimens in the sample representing *cinctum* are two males (C.N.H.M. No. 27219 and B.Y.U. No. 10404), both from near St. George, Washington County, Utah, with over-all dimensions of 485 mm., with the tail (160 mm.) comprising 0.49 of the snout-to-vent length in both. The largest female (M.V.Z. No. 10479, from Congress, Yavapai County, Arizona) has an over-all length of 475 mm., with a snout-to-vent length of 330 mm., the tail is not quite complete, but measures 145 mm., providing an approximate ratio of 0.45 for the tail/snout-vent.

Actually the two males and the female are of approximately the same over-all dimensions, the males having been hardened in preservative with the body distorted, whereas the female was preserved with the main axis of the body relatively straight, thus entailing less error in the measurements. Despite the difficulties in obtaining accurate measurements, it is reasonably certain that normally the tail of the male is a trifle longer, proportionately, than that of the female. Ratios calculated for the tail/snout-vent vary from 0.49 to 0.55, averaging 0.53, for males, and from 0.45 to 0.51 for females, with a mean of 0.49; juveniles are evidently similar to the females. Some of the variations in measurements obtained can be attributed to distortions of the body, the tail tending to be more flexible and easily measured. In consequence the

upper extremes as well as mean values obtained are somewhat higher than ratios that might be calculated from specimens measured prior to preservation. It should be noted that while the largest specimen of *H. s. suspectum* available exceeds in length the largest specimens of *cinctum*, the smaller sample of *cinctum* includes a higher percentage of individuals exceeding 300 mm. in snout-to-vent length.

Other proportions of *cinctum* are essentially

mediate in characters of scutellation. Those in which *suspectum* is virtually identical with *cinctum* are omitted in the following tabulation, which is based on 76 specimens of *suspectum* from the central and southern portions of its range, 17 more or less intermediate specimens of *suspectum* from the northern extremity of the range (Yavapai, Gila, and northeastern Maricopa counties in Arizona), and 27 specimens of *cinctum*:

	<i>H. s. suspectum</i>	Northern <i>H. s. suspectum</i> "Intermediates"	<i>H. s. cinctum</i>
1. With 2 postrostrals (Extremes 2-3)	84%	93%	92%
2. With 2 internasals (Extremes 2-3)	87%	88%	81%
3. With 3 canthals (Extremes 2-4)	94%	74%	81%
4. With 3 superciliaries (Extremes 3-5)	83%	76%	58%
5. Scales from occiput to internasals, mean (Extremes 11-15)	12.2 ± 0.14	12.7 ± 0.26	12.9 ± 0.19
6. With loreals: 2	29%	25%	41%
3	47%	19%	45%
4	21%	56%	14%
5	0	3%	0
7. With 2 preoculars	76%	81%	89%
8. Second supralabial reaching nasal	82%	69%	68%
9. Supralabials, mean (Extremes 10-14)	12.0 ± 0.09	12.0 ± 0.13	11.7 ± 0.11
10. Subcaudals, mean Extremes	52.8 ± 0.46 (48-59)	54.0 ± 0.76 (50-58)	57.3 ± 0.65 (52-62)
11. Lamellae under 4th toe, mean Extremes	10.8 ± 0.11 (8-13)	11.3 ± 0.16 (10-13)	11.6 ± 0.6 (9-14)

identical with those given for the nominate subspecies. The minor differences (table 1) can be attributed to the nature of the measurements or to other errors in sampling techniques.

SCUTELLATION: Except for minor differences, principally in frequencies or in mean values, the scale characters of *H. s. cinctum* are similar to those of *H. s. suspectum*. A summary of the characters is included in table 1. In this table, however, the data supplied for *suspectum* represent the entire sample, including specimens from the northern part of the range that bear closer resemblance in pattern characters to *cinctum* than do specimens from other portions of the range. As can be seen below, these specimens from the northern periphery of the range of *suspectum* are also inter-

In four of the 11 characters tabulated above percentages or means for the intermediates fall between those for *cinctum* and *suspectum*, more nearly resembling *suspectum* in the mean number of subcaudals. In two characters, the percentages with two internasals and the mean number of supralabials, they fall closer to *suspectum*. In three characters, the number of postrostrals, the number of scales between the occiput and the internasals, and the percentages having the second supralabial reaching the nasal, the intermediates are closer to *cinctum*. In the remaining two characters the intermediates differ from both races, more closely resembling *cinctum* in the number of canthals, but tending more often to have four. The northern *suspectum* tend to have four loreals more

often than the specimens in either of the other samples.

The Gila monsters inhabiting Yavapai, Gila, and northeastern Maricopa counties, Arizona, are thus somewhat arbitrarily referred to *H. s. suspectum*, largely because they represent the northern segment of a south-to-north trend in the pattern characters of that race. Despite some peculiarities, to be expected in any local population, it may be seen that in many respects the specimens are essentially intergrades, as noted in the description of the trends in pattern characters described for *H. s. suspectum*.

PATTERN AND COLORATION: The pattern of *cinctum* is subject to relatively little variation in its major features, even though no two specimens are identical. The majority of the individuals are like the type in all essential features. However, in a small percentage of the sample more mottling is present on the lighter (yellowish to orange or salmon pink) bands on the tail, and occasionally one of the "saddles" or double cross bars on the trunk may be partly confluent with an adjacent one; that is, the margin of one may have an extension that connects it to an adjacent one.

The ontogenetic changes in pattern are minor, consisting principally in the acquisition of some mottling in both the light and dark bands on the tail, as well as on the lower limbs, which were uniformly black or dark brown in the hatchling. Also a few pink or yellow scales may appear near the middle of the black areas comprising the borders of the saddles. To judge only by the preserved material, there is some tendency for the ground color to be very pale yellow in juveniles and pinker or orange in adults.

HABITAT

Virtually nothing concerning the habitat of the Gila monster within the range of *cinctum* has been reported. Woodbury (1928) notes that it "usually lives in the rock ledges," in and near Zion National Park, but records for this area have not been confirmed. Woodbury (1931) lists Santa Clara Valley and St. George but omits Zion National Park from his list of localities for Utah in a later paper and states "This poisonous lizard lives mostly around the ledges and rocky places unfrequented by man." A specimen taken by R. Woodbury on June 10, 1939 (U.U. No. 1932), 5 miles west of Hurri-

cane, at Berry Springs in Washington County, Utah, has a note on the tag that it was taken "on a rocky ridge."

In view of the fact that much of the region inhabited is characterized by a rocky terrain, it is not astonishing that Gila monsters are more often found in rocky places. It seems doubtful, however, that they are so restricted. The type, from Las Vegas, is from the periphery of the range in Nevada where the species is certainly not abundant. However, Gila monsters may have been more commonly seen prior to the settlement of the Las Vegas Valley, where the terrain is relatively flat, sandy, and characterized by creosote bush, mesquite, and Spanish dagger (*Yucca mohavensis*). The town of Las Vegas lies at the site of several natural springs. It is not impossible that *cinctum* is restricted to the vicinity of springs or streams, which may account for its scarcity or probable absence in much of the territory between the stations within its general range. It is doubtful whether it occurs in many localities west of the region having a minimum warm-season precipitation of 2 inches (as mapped by the United States Department of Agriculture, 1941), although most of the range of *cinctum* is characterized by greater aridity than the region occupied by the nominate subspecies.

The mean annual precipitation at Las Vegas for a period of 31 years is only 4.85 inches, of which 2.26 inches falls during the warm season, April to September. Las Vegas lies at an elevation of 2033 feet. St. George, Utah, the source of most of the specimens from Utah, lies in the valley of the Virgin River at an elevation of 2800 feet, where the mean annual precipitation for a 40-year period averages 8.73 inches, of which 3.62 inches are received during the warm season. Wickenburg, the source of many specimens representing *cinctum* from the state of Arizona, lies on the Hassayampa River, a tributary of the Gila, at an elevation of 2072 feet. At Wickenburg the mean annual precipitation for a 40-year period is 10.89 inches (H. V. Smith, 1945), with nearly 5 inches of rain during the warm season. As in other portions of the desert, the precipitation in all these localities is subject to considerable fluctuation from year to year, and there is no marked difference in this respect between the region occupied by *cinctum* and that inhabited by *suspectum*.

As far as the vegetation is concerned, *cinc-*

tum, as does the nominate race, occurs in regions characterized by such xerophytic plants as paloverde (*Cercidium* and *Parkinsonia*), cactus, creosote bush, and mesquite, principally between the elevations of 2000 and 3000 feet above sea level.

RANGE

The banded Gila monster is confined to the drainage of the Colorado River, in western Arizona, extreme southeastern Nevada, and southwestern Utah. More specifically it is known to occur east of the Colorado River from the Kofa Mountains in central Yuma County, Arizona, northeastward to the edge of the Central Plateau in southwestern Yavapai County, and from there north and west across the Colorado River to Clark and Lincoln counties in Nevada and in Washington County in the adjacent portion of extreme southwestern Utah.

The range of *cinctum*, like that of other members of the genus, does not conform to boundaries mapped for deserts or biotic provinces. It inhabits portions of the Sonoran, Mojave, and Great Basin deserts as mapped by Shreve (1942), and inhabits the central portion of the "Sonoran Biotic Province" as well as the eastern edge of the "Mohavian province" as mapped by Dice (1943). As does *H. s. cinctum* it occurs principally within the Lower Sonoran Life Zone, extending into a juniper-piñon belt of the Upper Sonoran Zone.

LOCALITY RECORDS

Specimens now referable to *cinctum* were collected at a relatively early date, although few of them found their way into collections. Baird's (1859b) record (as "*Heloderma horridum*") from the "Mohave river" presumably referring to the stream in San Bernardino County, California, is doubtless in error, although the data may originally have been abbreviated as "Mojave R" and intended to designate the [Fort] Mojave [Indian] R[eservation] (rather than "River") in western Arizona, where *cinctum* is to be expected. Cope (1866), also under the name *horridum*, lists a specimen from Fort Whipple, which lies at an elevation of 5400 feet in the mountains of Yavapai County, Arizona. However, Coues (1875) indicates that this specimen was actually taken in the vicinity of La Paz on the Colorado River in Mohave County. Cope's brief description,

"Yellow orange, the black cross bars parallel and connected [*sic*] margins of orange spots," aptly if ungrammatically describes *cinctum*. The record is partly substantiated by the occurrence of the race in the Kofa Mountains to the southeast, as well as by a head from "150 miles up the Colorado River from Yuma" in the collection of the San Diego Society of Natural History.

Yarrow, in 1875, reported a specimen of *Heloderma suspectum* from Mt. Turnbull [in northeastern Graham County, Arizona, and hence referable to *H. s. suspectum*] collected September 19, 1873, by E. Sommer. Presumably this is the same specimen later listed (by Yarrow, 1882, and by Cope, 1900, p. 483, for examples) as collected by "G. H. Sommer, Sept. 19, 1874" and as having come from "Mount Trumbull," which rises to 7700 feet in the Uinkaret Mountains north of the Grand Canyon in Mohave County, Arizona. The latter locality, even the foothills at 6000 feet, is at a higher elevation than any where *cinctum* is known to occur. The specimen, presumably the one mentioned by Yarrow, is now (U.S.N.M. No. 8454) catalogued as being from "Mount Trumbull," but must be the specimen originally listed from Mt. Turnbull; it definitely is referable to *H. s. suspectum*. The similarity in the names of the two mountains doubtless has caused the confusion. Cope (1900) mentions a specimen sent to him from St. Thomas, "Arizona," presumably in error for Nevada, as there is no St. Thomas in Arizona.

In the following list we have included all records drawn from the literature that we believe to be authentic, as well as records based on specimens examined. The specimen from "150 miles up the Colorado River from Yuma" probably is from Mohave County, Arizona. However, the data are not sufficiently precise to be certain that the specimen did not come from the western side of the river, in California. Thus far there is no evidence that *Heloderma* actually occurs in California. Its occurrence in Nevada west of the Colorado River suggests the possibility that it may yet be found in the Whipple or Chemehuevis Mountains north of Parker. Such records as the indefinite one mentioned, as well as those not based on specimens examined by trained specialists, are included with an element of doubt, as indicated in the list as well as on the

map by means of the question mark. Records for Zion National Park recorded by Woodbury (1928), but by implication rejected by Woodbury (1931), are excluded. Approximate elevations for localities listed are given in parentheses whenever reliable information could be obtained. It may be noted that the majority of specimens are from habitats between 2000 and 3000 feet, with at least one specimen from Congress, in Yavapai County, from 3688 feet above sea level.

Specimens in addition to the type listed by catalogue number provide the basis for the description and the summary of variations and hence are herewith designated as paratypes. The fragments of skin and osteoderms reported from Gypsum Cave, 15 miles east of Las Vegas in Clark County, Nevada, by Brattstrom (1954) are said to be from deposits estimated to be 8000 to 10,000 years of age. Whether these fragments can be assigned to the race *cinctum* is problematical, but it is doubtful whether there have been important changes in the population of *Heloderma* in southern Nevada within the past 10,000 years. The inclusion of Brattstrom's record in the following list of localities does not imply, however, that the fragments can be assigned with certainty to the subspecies now inhabiting the region. (Map 2.)

NEVADA

Lincoln County

Meadow Valley, Van Denburgh, 1922, p. 473

Clark County

Valley of the Virgin River, 8 miles below Bunkerville, U.S.N.M. No. 18640 (fragments only)

Overton (1360 ft.), Cowles and Bogert, 1936, p. 39

St. Thomas (1150 ft.), Van Denburgh, 1922, p. 473

Las Vegas (2033 ft.), A.M.N.H. No. 7456 (type)

Gypsum Cave (ca. 2000 ft.), Brattstrom, 1954, p. 10

UTAH

Washington County

Berry Springs, 5 miles west of Hurricane, U.U. No. 1932

St. George (2800 ft.), U.U. No. 2030, B.Y.U. Nos. 10403, 10404, C.N.H.M. No. 27219, M.C.Z. No. 4315

Near St. George (2800 ft.), U.U. No. 2810

Red Hill, St. George (2800 ft.), U.U. No. 2647

UTAH

Washington County

4.6 miles southwest of St. George (2800 ft.), M.V.Z. No. 49994

Near Washington Fields Dam (2720 ft.), U.U. No. 2811

Bloomington (ca. 2800 ft.), L.M.K. No. 25599

Santa Clara Valley (2700 ft.), Van Denburgh, 1922, p. 473

ARIZONA

Mohave County

Pierce Ferry (ca. 1500 ft.), C. H. Lowe, field no. 4871

?Diamond Canyon, Hualpai Reservation, Woodson, *in litt.*, sight record of J. E. Hogg

Near Kingman (3435 ft.), Woodson, *in litt.*, sight record of C. E. Dailey

Oatman (2200 ft.), Woodson, *in litt.*, sight record of J. L. Barritt

? "150 miles up Colorado River from Yuma," [presumably in Mohave County], S.D.N.H.S. No. 11367 (head only)

Yavapai County

Base of Yarnell Hill (3500 ft.), Woodson, *in litt.*

4 miles south of Yarnell (3500 ft.), Woodson, *in litt.*

Congress (3688 ft.), M.V.Z. Nos. 10478, 10479

Congress Junction (3050 ft.), Woodson, *in litt.*

10 miles east of Congress Junction (3200 ft.), F.A.S. No. 2991

Maricopa County

Wickenburg (2072 ft.), C.N.H.M. No. 8468

Vicinity of Wickenburg (2100 ft.), F.A.S. Nos. 2719, 2992, 2994, 1 specimen without number

1 mile west of Wickenburg (2100 ft.), F.A.S. No. 1739

One-half mile west of Wickenburg (2100 ft.), F.A.S. No. 2996

2 miles west of Wickenburg (2100 ft.), F.A.S. No. 2993

5 miles southwest of Wickenburg (2100 ft.), F.A.S. No. 937

12 miles southwest of Wickenburg (2100 ft.), F.A.S. No. 1779

Yuma County

Near La Paz on the Colorado River, Coues, 1875, p. 602

Kofa Mts., Kofa Game Refuge, U.S.N.M. No. 129064

TABLE 1
SUMMARY OF CHARACTERS OF LIZARDS OF THE GENUS *Heloderma*
(Means are followed by their standard error.)

	<i>H. h. alvarezii</i>	<i>H. h. horridum</i>	<i>H. h. exasperatum</i>	<i>H. s. suspectum</i>	<i>H. s. cinctum</i>
Number of specimens ^a	7	31	16	93	27
Source of sample	Chiapas	Oaxaca to Sinaloa	N. Sinaloa to S. Sonora	Sonora, S. Arizona, New Mexico	W. Arizona Nevada, Utah
Number of postrostrals, percentage having					
1	—	5	—	—	—
2	100	82	73	90	92
3	—	—	20	10	8
4	—	13	7	—	—
Number of internasals, percentage having					
2	100	95	93	87	81
3	—	5	7	13	19
Number of canthals, percentage having					
2	10	—	23	1	2
3	90	98	70	91	81
4	—	2	7	8	17
Number of superciliaries, percentage having					
1	—	2	—	—	—
2	—	8	20	—	—
3	88	84	77	83	58
4	12	5	3	16	40
5	—	—	—	1	2
Number of scales from occiput to internasals					
Mean	8.4 ± .5	9.7 ± .3	10.9 ± .2	12.5 ± .1	12.9 ± .2
Extremes	(7-9)	(7-12)	(10-12)	(11-15)	(11-15)
Number of scales across head between poster- ior superciliaries ("in- terorbitals"), per- centage having					
6	80	32	—	—	—
7	20	45	—	65	58
8	—	18	100	35	42
9	—	5	—	—	—
Number of loreals, per- centage having					
1	57	28	10	—	—
2	43	67	57	41	41
3	—	5	33	36	45
4	—	—	—	22	14
5	—	—	—	1	—
Number of lorilabials					
Mean	4.9 ± .1	5.1 ± .1	4.5 ± .1	5.7 ± .1	6.1 ± .2
Extremes	(4-5)	(4-7)	(4-6)	(4-9)	(4-12)

^a The figures given represent the total number of specimens available, excluding skeletal material (tabulated separately). However, all characters could not be ascertained on individual specimens.

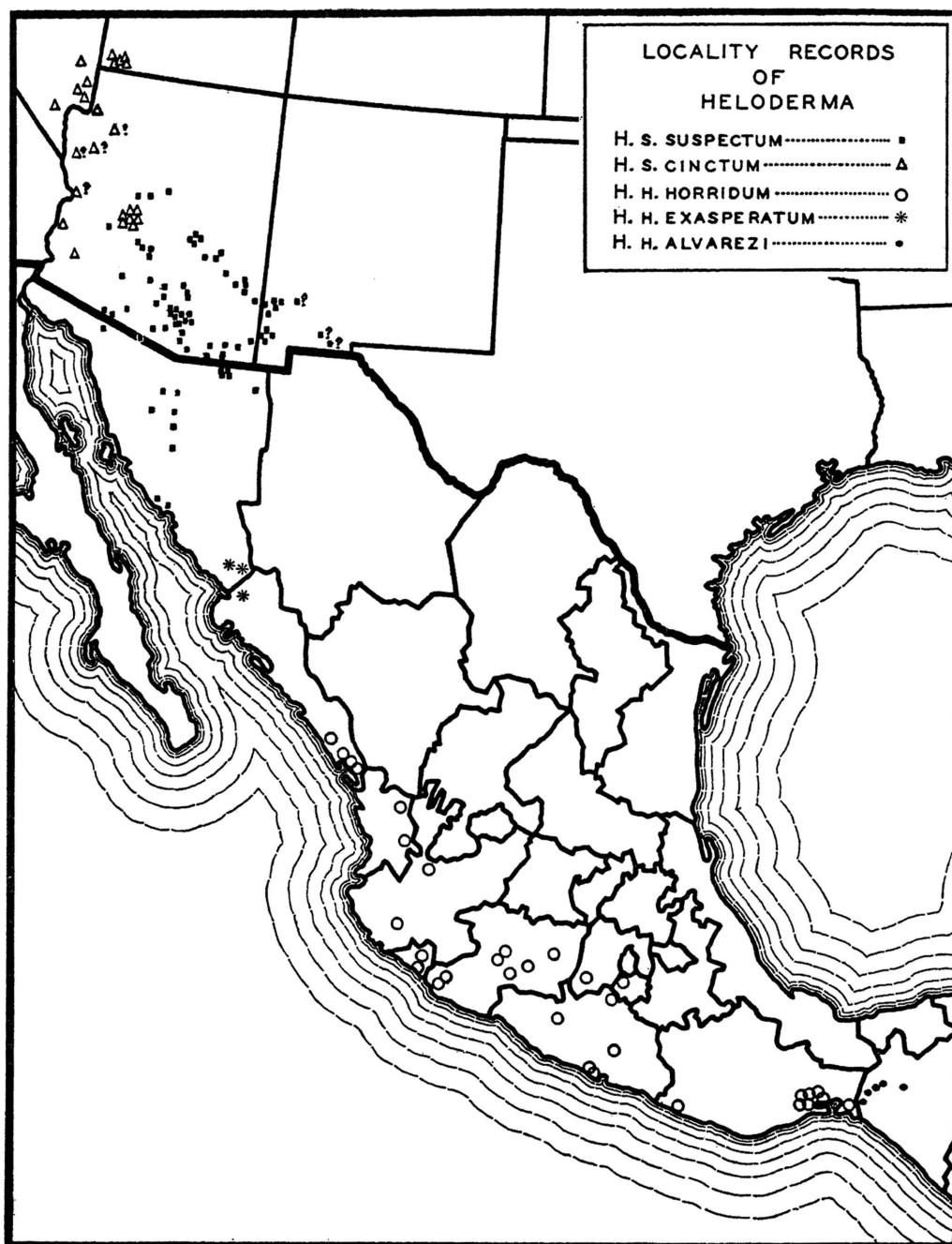
TABLE 1—(continued)

	<i>H. h. alvarezi</i>	<i>H. h. horridum</i>	<i>H. h. exasperatum</i>	<i>H. s. suspectum</i>	<i>H. s. cinctum</i>
Number of preoculars, percentage having					
1	—	12	7	23	11
2	100	88	93	73	89
3	—	—	—	4	—
Percentage having su- pranasal separated from postrostral	100	95.9	3.3	100	100
Percentage having 2d supralabial reaching nasal or prenasal	0	35	100	82	68
Number of supralabials					
Mean	10.6 ± .1	11.1 ± .1	11.3 ± .1	12.0 ± .1	11.7 ± .1
Extremes	(10-11)	(10-13)	(10-13)	(10-14)	(10-13)
Number of infralabials					
Mean	12.2 ± .3	13.0 ± .1	13.5 ± .1	14.3 ± .1	14.1 ± .1
Extremes	(11-14)	(11-15)	(12-15)	(12-16)	(12-16)
Number of infralabials reaching chin-shields, percentage having					
1	—	10	13	95	100
2	100	90	87	5	—
Mental, percentage having					
Shield shaped	—	36	100	—	—
"Modified shield"	—	28	—	—	—
Wedge shaped	100	36	—	100	100
Pairs of enlarged chin- shields in contact, percentage having					
2	57	54	—	—	—
3	43	46	100	90	89
4	—	—	—	10	11
Number of transverse rows of ventrals, gu- lar fold to vent					
Mean	62.1 ± .9	63.0 ± .4	65.3 ± .9	66.0 ± .3	66.6 ± .4
Extremes	(60-67)	(59-68)	(61-73)	(60-72)	(64-71)
Number of transverse rows of ventrals, ax- illa to groin					
Mean	49.1 ± .3	50.7 ± .5	51.9 ± .5	52.9 ± .2	52.2 ± .5
Extremes	(48-50)	(45-56)	(49-57)	(48-59)	(49-57)
Number of scales around midbody					
Mean	52.4 ± .9	54.9 ± .5	56.8 ± .5	57.0 ± .2	57.5 ± .3
Extremes	(49-56)	(51-58)	(54-60)	(52-62)	(54-60)
Number of subcaudals					
Mean	78.2 ± 1.3	80.2 ± .7	80.4 ± .6	52.8 ± .4	57.3 ± .7
Extremes	(73-82)	(74-87)	(77-85)	(48-59)	(52-62)
Number of scales around base of tail					
Mean	26.3 ± .9	29.1 ± .5	30.3 ± .5	27.9 ± .2	28.3 ± .3
Extremes	(24-31)	(26-35)	(27-34)	(26-31)	(26-31)

TABLE 1—(continued)

	<i>H. h. alvarezi</i>	<i>H. h. horridum</i>	<i>H. h. exasperatum</i>	<i>H. s. suspectum</i>	<i>H. s. cinctum</i>
Number of lamellae under 4th toe					
Mean	13.2 ± .1	13.1 ± .1	13.6 ± .1	11.1 ± .1	11.6 ± .2
Extremes	(13-14)	(11-15)	(12-15)	(8-13)	(9-14)
Enlarged preanal scales	Absent	Absent	Absent	Present	Present
Head width at eye/head length (mean and extremes)					
♂	.58(.55-.61)	.59(.53-.62)	.61(.57-.64)	.58(.58-.60)	.56(.52-.58)
♀	.63(.60-.65)	.60(.55-.63)	.61(.59-.64)	.57(.54-.61)	.57(.53-.58)
J	.73(.73)	.58(.56-.63)	—	.57(.52-.62)	.55(.52-.57)
Head length/snout-vent length (mean and extremes)					
♂	.19(.19)	.20(.19-.22)	.18(.16-.20)	.18(.16-.21)	.18(.16-.19)
♀	.17(.16-.17)	.18(.17-.19)	.18(.17-.18)	.17(.16-.19)	.17(.16-.19)
J	.18(.18)	.21(.20-.21)	—	.18(.15-.20)	.18(.17-.19)
Tail length/snout-vent length (mean and extremes)					
♂	.82(.81-.83)	.84(.80-.88)	.76(.70-.77)	.47(.45-.52)	.53(.49-.55)
♀	.75(.73-.79)	.75(.72-.80)	.73(.71-.74)	.48(.45-.51)	.49(.45-.51)
J	.65	.72(.67-.78)	—	.45(.41-.49)	.49(.45-.52)
Hind leg span/snout-vent length (mean and extremes)					
♂	.70(.70)	.76(.72-.79)	.75(.71-.77)	.69(.63-.73)	.71(.66-.76)
♀	.65(.65)	.74(.70-.77)	.72(.70-.74)	.68(.63-.73)	.66(.65-.68)
J	—	.75(.72-.79)	—	.69(.65-.75)	.70(.66-.74)
Length of claw (4th finger), as percentage of snout-vent length					
♂	2.7(2.7)	3.0(2.6-.33)	2.7(2.4-3.1)	2.0(1.5-2.6)	1.8(1.4-2.4)
♀	2.4(2.2-2.7)	2.9(2.5-3.6)	2.9(2.6-3.2)	2.1(1.9-3.0)	1.4(1.2-1.5)
Length of claw (4th toe), as percentage of snout-vent length					
♂	2.3(2.3)	2.4(2.0-2.8)	2.1(1.9-2.2)	1.2(1.0-1.4)	1.5(1.0-2.1)
♀	1.8(1.7-2.0)	2.4(1.8-3.0)	2.4(2.3-2.5)	1.4(1.0-1.6)	1.3(1.0-1.4)
Maximum size in mm.					
Total length					
♂	650	745 ^b	775	520	485
♀	635	690	715	485	475
Snout-vent					
♂	355	410 ^b	455	349	325
♀	365	390	410	325	330
Black tail bands, percentage having					
4	—	—	—	31	—
5	—	—	—	69	100
6	100 ^c	62	43	—	—
7	—	38	57	—	—

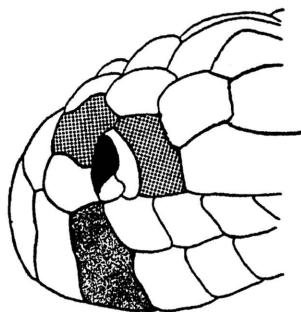
^b Estimates based on largest head only.^c Black "bands" separated by vestiges of paired white "bands" discernible only on under side of tail in adults.

MAP 2. Locality records of *Heloderma*.

KEY TO THE FOSSIL AND RECENT LIZARDS OF THE GENUS *HELODERMA*

- I. Posterior portion of maxilla (all represented) with outer surface granular (known only from Oligocene deposits in Logan County, Colorado). . . †*Heloderma matthewi* Gilmore
- II. Posterior portion of maxilla with outer surface of maxilla relatively smooth, with slight striations (osteoderms firmly ankylosed conceal surface in adults).
 - A. Tail comprising from 41 to 55 per cent of snout-to-vent length; 48 to 62 transverse rows of scales on under side of tail posterior to vent; a pair of enlarged preanal scales (fig. 2); one pair of infralabials reaching chin-shields (fig. 6); juveniles with four or five black bands (including black terminus on tail); eight or nine maxillary teeth; upper posterior process of splenial extended onto inner surface of coronoid. *H. suspectum* Cope
 - a. Adult with dorsal pattern consisting of four "saddles" or irregular, double black bands (each containing a row of pink or yellow circular areas), few or none of which are confluent with adjacent saddles; tail with five distinct black bands (including black terminus), sparsely if at all dotted with yellow, which alternate with pink or yellowish bands that may contain a few isolated clumps or short rows of black scales, with the black bands approximately the same width as the intervening light areas. Range: Extreme southeastern Nevada, southwestern Utah, southward through western Arizona. *H. s. cinctum*, new subspecies
 - b. Adult with dorsal body pattern consisting of a black (or dark brown) reticulum enclosing pink or yellowish areas, the darker color predominating; tail with four or five irregular dark bands mottled or streaked with pink or yellow, which alternate with pink or yellowish bands streaked or mottled with black or dark brown. Range: Central Arizona southeastward along the edge of the Plateau to southwestern New Mexico, southward through the Mexican state of Sonora at least as far as Guaymas. *H. s. suspectum* Cope
 - B. Tail comprising at least 65 per cent of snout-to-vent length; 72 or more trans-

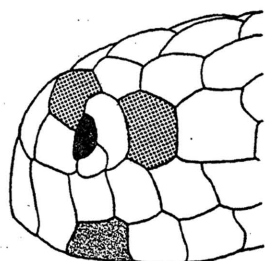
verse rows of scales on under side of tail posterior to vent; no pair of enlarged preanal scales present (fig. 3); usually two pairs of infralabials reaching chin-shields (fig. 7); juveniles with six or seven black bands (including black terminus) on tail; six or seven maxillary teeth; upper posterior process of splenial reaching, but not overlapping, coronoid.
 *H. horridum* Wiegmann



H. h. exasperatum

FIG. 10. Diagram showing the position of the scales on the snout of *Heloderma horridum exasperatum*, with the supranasal in contact with the postnasal and the second supralabial reaching the prenasal. Compare with figure 11.

- a. Supranasal in contact with postnasal (fig. 10); eight scales separating posteriormost superciliaries across the head; pattern on body of adults consisting of a black reticulum (sometimes a black ground color) enclosing lighter (yellowish, reddish, or pinkish) areas that equal or exceed the black in extent; irregular but discernible light and dark bands on tail narrow, one or two scale rows wide, roughly equal in width. Range: The Río Fuerte drainage basin of southeastern Sonora and northern Sinaloa in México.
 *H. h. exasperatum*, new subspecies
- b. Supranasal separated from postnasal by first canthal (fig. 11); usually six or seven scales separating superciliaries across crown of head.
 1. Pattern of adult with black color predominating, but enclosing blotches, bars, or dots (usually with all three present); six or seven pairs of light bands on tail, with or without a light



H. h. alvarezi

FIG. 11. Diagram showing the position of the scales on the snout of *Heloderma horridum alvarezi*, with the supranasal separated from the postnasal by the first canthal, and the second supralabial excluded from contact with the nasal and prenasal by a lorilabial.

bar or band in the intervening black band. Range: The Pacific slope of México from southern Sinaloa southeastward to eastern Oaxaca.

. *H. h. horridum* Wiegmann

2. Pattern on dorsum almost uniformly black in the adult, with faint vestiges of bars or a few dots sometimes present, vestiges of six pairs of light bands on tail usually discernible on under side only. Range: The Atlantic drainage of central Chiapas, principally the headwaters of the Río Chiapa in extreme southern México, possibly eastward into Guatemala.

. *H. h. alvarezi*, new subspecies

CLINES IN *HELODERMA*

THE RELATIVELY SIMPLE distributional pattern of the Recent species and subspecies of *Heloderma*, with their ranges roughly in linear sequence between the latitudes of 16° and 37° N., through an airline distance of approximately 3200 kilometers (ca. 2000 miles), makes the group ideal from some standpoints for a study of inter-group trends in variation. As now demonstrated for many groups of organisms where features of the environment in the regions inhabited change gradually over a wide area, there is often a corresponding gradual change in characters measurable at the population level. Such character gradients have been called clines by Huxley (1938) in a preliminary paper greatly elaborated in 1939. As he points out, the naming and description of subspecific forms, however necessary, are not sufficient. Mere pigeonholing of populations has the disadvantage of conveying a false impression of uniformity and of focusing undue attention on named populations as against those that remain unnamed.

However, the real significance of clines lies not so much in their bearing on taxonomic procedures as in the use of data derived from their study in dealing with problems of natural selection. For clines reflect the response of the population to small climatic differences (as well as to other environmental factors), as shown by more recent studies in addition to those already cited by Huxley (1939). There are, of course, few regular trends in environmental factors, much less in microhabitats; as a possible corollary Mayr (1942, p. 96) notes that the majority of clines represent only the averages of fluctuating trends in morphological attributes. This is true of several characters in *Heloderma*, although the lack of adequate series representing local populations precludes the possibility of our investigating this aspect of the problem to any significant extent.

Most investigations dealing with clines in land-dwelling animals have dealt with only one or a few characters. Usually there has been an attempt to correlate progressive changes in morphological characters with changes in temperature, humidity, or the color of the soil. Whereas the use of a limited number of charac-

ters greatly simplifies the presentation and interpretation of the results, it may be assumed that, as with the pigeonholing of races, this procedure also obscures portions of the picture that may be of equal or even of greater significance.

In this investigation, therefore, we have attempted to consider a number of characters. Further complexities are admittedly introduced, more especially as it is obvious in evaluating differences, as Klauber (1945b) points out, that greater weight should be given to several independent characters than to the same number of correlated characters. To cite an example, in *Heloderma* one of the more obvious differences between the two living species is the difference in proportionate tail length. As might be anticipated, the species with the relatively longer tail also has more caudal vertebrae and more rows of scales encircling the tail. It is conceivable of course that the species with the shorter tail may have had a similar number of scales and vertebrae that were relatively shorter than those of the long-tailed species. But in any event, it seems plain that there would have been some sort of correlation in the characters, and whereas three characters are tabulated, these are in reality manifestations of a single difference, namely, the relative tail length.

We know nothing of the genetic basis of the characters in *Heloderma*, nor is there much hope that such information can be obtained. Despite our efforts to study individual characters, it is assumed, of course, that evolutionary changes have affected the organism as a whole, not merely its individual parts.

To simplify the presentation of data we have made use of graphic methods whenever possible, although these are supplemented by the data in table 1. To show the nature of the trend in some characters we have used simple bar diagrams. For others we have employed the Dice-Leraas method with the modification suggested by Hubbs and Perlmutter (1942), using graphs that show: (1) the total range of variation on a horizontal line; (2) one standard deviation on each side of the mean by a black rectangle; (3) twice the standard error on each

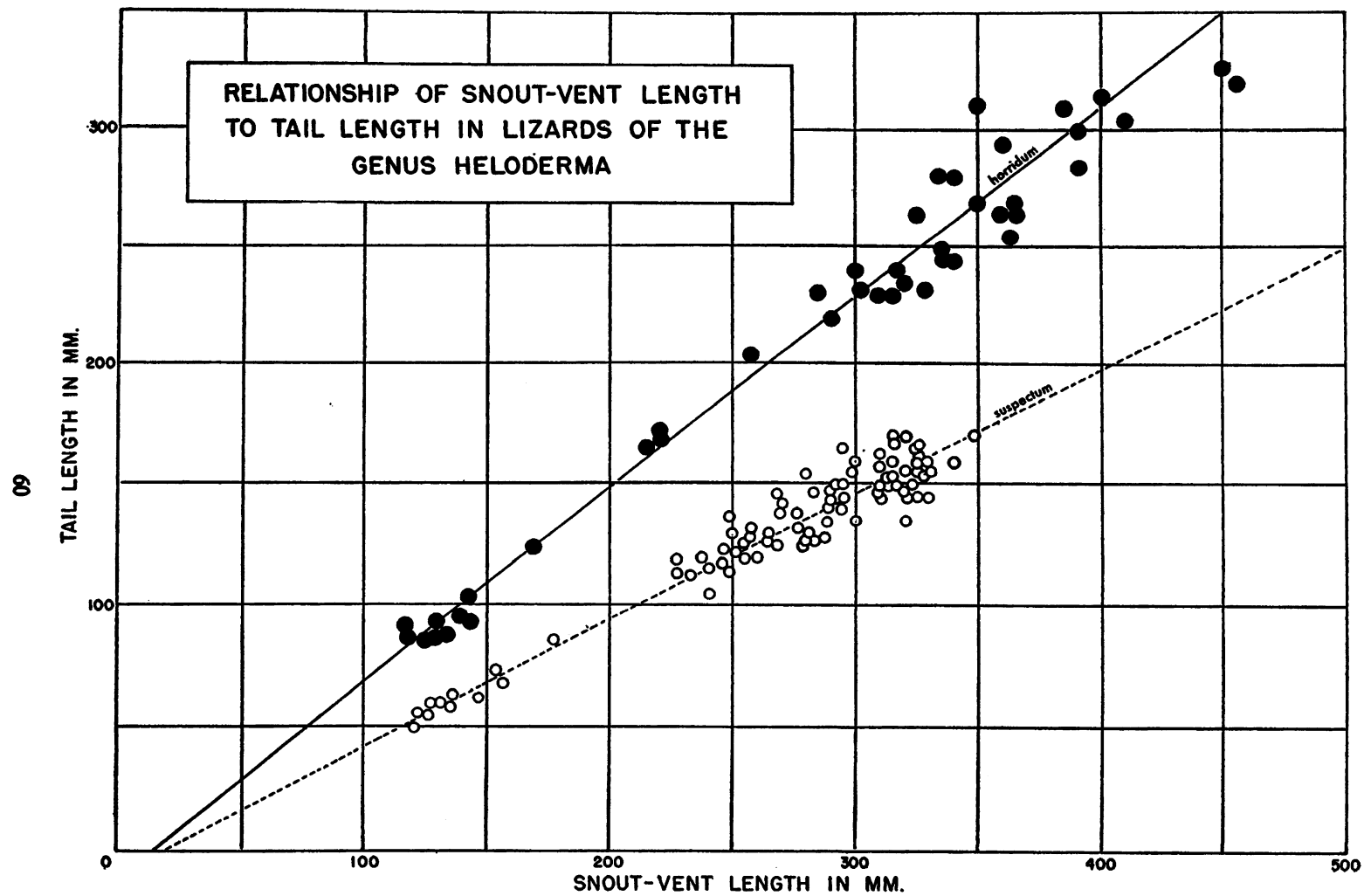


FIG. 12. Diagram showing differences between species in proportionate tail length, as well as size groups represented in samples.

side of the mean in an open rectangle; and (4) the mean, indicated by a vertical line.

For the most part the characters tabulated (table 1) are those commonly used in systematic work with lizards. Few taxonomic studies of saurian genera have made use of as many characters. Commonly fewer are needed to demonstrate differences between races or species. Indeed many of those tabulated are of little or of no value in segregating the subspecies recognized. Our tabulations are, of course, not exhaustive. Many other characters might well have been included, and our choice of those used has been guided largely by the practical considerations of whether counts could easily be made or whether they could be duplicated by other persons. Such characters as the shape of the mental scute or the sort of pattern observed on the tail admittedly involve subjective interpretations, and somewhat arbitrary decisions must be made in borderline cases. Nevertheless table 1 and the graphs reflect with reasonable accuracy the trends shown by the samples available.

Because of the complexities resulting from

mens the minimum for dependable results), we have omitted characters of proportionality from this discussion of clines. Summaries of the data obtained for such characters are, however, presented in table 1. We have plotted regression lines (fig. 12) showing the relationship of the tail length to the snout-to-vent length for the two species. We have not attempted to show differences between the subspecies, as far as this relationship is concerned, although the data presented in table 1 suggest that such differences exist and that marked changes in the relative length of the tail occur during the ontogeny of the subspecies of *horridum* that are doubtfully present in the races of *suspectum*.

It is pertinent to note that, aside from differences between the two Recent species in proportions, there are dichotomous differences in some characters of the scutellation, dentition, and skeleton that are not subject to enough variation, at least as far as our data indicate, to warrant their use in a discussion of intra-specific trends. Differences of the sort between the two species may be summarized as follows:

CHARACTER	<i>H. horridum</i>	<i>H. suspectum</i>
Pair of enlarged preanal scales	Absent	Present
Maxillary teeth	6 to 7	8 to 9
Palatine teeth	Present	Absent
Posterior process of splenial	Reaching coronoid (fig. 4)	Overlapping coronoid (fig. 5)
Caudal vertebrae	40	24 to 28

ontogenetic changes, possible sexual dimorphism, and the resulting lack of adequate samples when sexes and sizes are considered separately (see Klauber, 1943, who considers 25 speci-

There is no overlap between the species in some other characters despite the existence of variations subject to geographical trends within the species.

TRENDS IN CLIMATIC FACTORS

Before the characters that illustrate the phenomena of clines are discussed, it is desirable to summarize such information as we have been able to obtain concerning climatic factors within the ranges of each of the five subspecies of *Heloderma*. There is little correlation of the distributions of the subspecies and the boundaries of climatic provinces, as mapped by Thornthwaite (1931), Arias (1942), or by Tamayo (1949), who includes a map for México based on Thornthwaite's classification as well as one based on the Köppen system. Simi-

larly, there is little evidence of any marked correlation of habitats and vegetation, as mapped by Arias (*supra cit.*) or by Leopold (1950). Inasmuch as we have no data concerning microhabitats, we have been forced to use the climatic data assembled by meteorologists, principally those published by Arias for México and those of H. V. Smith (1945) and the United States Department of Agriculture (1941) for the United States.

To obtain the information shown graphically in figure 13 we have plotted averages of mean

annual temperatures and averages of the means for annual precipitation of representative stations within the range of each of the five subspecies. Also, in view of the fact that the activities of the lizards of the genus are largely restricted to the wet season, we have plotted the averages of the means for the temperature and calculated means for the total rainfall during the four months of the year that encompass the season of maximum precipitation for the stations within the range of each race. From St. George, Utah, southward to Mazatlán, Sinaloa, the wet season is ordinarily from July to October, inclusive; south of Mazatlán the bulk of the precipitation within the range of *Heloderma* is received during the four-month period June to September, inclusive.

In so far as possible we have tried to include peripheral stations and to restrict the localities represented in the data to those from which we have seen specimens. The number of stations represented for each race is indicated (in parentheses) followed by the range of altitude (in meters) of the stations for which data are available, as follows: *alvarezi* (2), 536 to 545 m.; *horridum* (6), 3 to 1538 m.; *exasperatum* (3), 71 to 508 m.; *suspectum* (7), 3 to 1110 m.; and *cinctum* (4), 620 to 1124 m. The range in latitude of the stations plotted is indicated on the graph.

In order to show the general trends more clearly in figure 13 we have connected the averaged means calculated for the stations within the range of each subspecies. As far as temperature and precipitation are concerned it will be noted:

1. That there is a general increase in wet-season temperatures from the southeast to the northwest as far as southern Sonora, but a reversal in the trend from Sonora to Utah and Nevada within the ranges of *suspectum* and *cinctum*. It is possibly significant that temperatures below freezing have not been recorded at any locality within the range of *horridum* and its races, although temperatures have dropped to as low as 0.5° C. at Minas Nuevas in southern Sonora, the northern periphery of the range of the species. However, temperatures below zero on the Centigrade scale have been reported for virtually all stations within the range of *suspectum* and *cinctum* to the north, with the exception of localities near Guaymas on the

coast of Sonora. Cold winters north of central Sinaloa are reflected in the drop in mean annual temperatures. In view of the fact that lizards of the genus *Heloderma* are not active during dry seasons or at temperatures much below 24° C., it is doubtful whether mean annual temperatures are of great importance. It is possible, however, that higher annual temperatures within the range of *horridum* and its races permit these lizards to be abroad for longer periods than either *suspectum* or *cinctum* to the north.

2. That there is a general trend towards increasing aridity from the range of *H. h. horridum* northward, although the territory occupied by *alvarezi*, in a "rain shadow" on the Atlantic drainage of Chiapas, receives somewhat less rainfall than the average for localities inhabited by *horridum*. Moreover, it will be noted that there is considerably less moisture available to *exasperatum* than to the two populations to the south. The close parallel between the mean wet-season precipitation and the precipitation for the entire year reflects the existence of a well-defined wet season throughout the territory now inhabited by *Heloderma*, with a deficiency in precipitation for the remaining two-thirds of the year. In the arid and semi-arid regions inhabited by *suspectum* there is, of course, a deficiency in precipitation throughout the year. It is almost certainly significant, however, that most of the available moisture is received during the warm season. In fact, we venture to suggest that the absence of *Heloderma* in the deserts of California is attributable to the fact that west of the Colorado River summers are dry, with most of the precipitation occurring during the winter months.

At the north thermal factors probably restrict the dispersal of *Heloderma*. Where suitable summer temperatures prevail in much of the desert west of the state of Arizona, the lack of moisture must be the limiting factor. It seems manifest that the extent of the range of many species of reptiles is dependent on different factors in different areas. In the case of *Heloderma* there is, in effect, an interaction of moisture as well as temperature factors, and when suitable levels of each are not reached simultaneously in a given region, it becomes uninhabitable by such lizards as helodermatids.

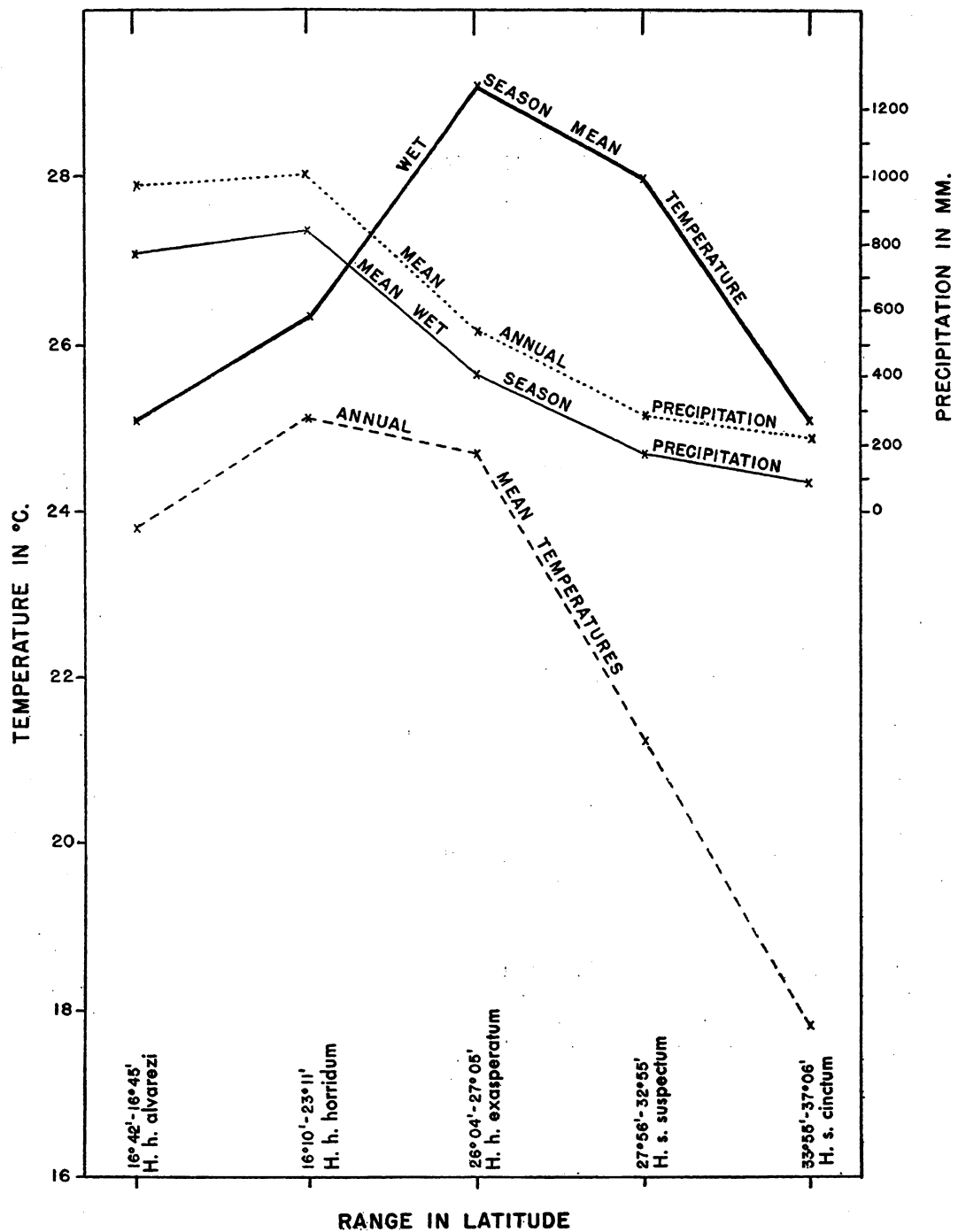


FIG. 13. Graph showing climatic trends within the areas occupied by lizards of the genus *Heloderma*. For explanation, see text.

(See Odum, 1953, for a reconsideration of Leibig's "Law.")

It may not be without significance that the mean for average wet-season temperatures pre-

vailing within the range of *cinctum* at the north is within a fraction of a degree of that for wet-season means within the range of *alvarezi* at the south.

TRENDS IN CHARACTERS

In the following discussions we shall attempt to amplify and interpret the data shown graphically in figures 14 to 29. It should be emphasized that we are interested here in showing the gradations in geographic variations; we are not concerned with the significance of the differences between populations from the taxonomic viewpoint, even though taxonomic implications are inevitably included in the discussion. The characters being considered are summarized under headings similar to those used in the taxonomic section, where the variations encountered in the samples are described in greater detail.

SIZE

Although there can be little doubt that the size of most organisms is subject to natural selection, it is a character difficult to evaluate in studies of reptiles. Klauber (1945b) has discussed the problems involved as far as snakes are concerned, and virtually all of his comments are applicable to studies of lizards, or at least to the helodermatids. As he points out, we are handicapped by a slow but continued growth in many adult reptiles, in contrast to the essentially static condition characteristic of adult birds and mammals. Moreover, as Klauber also notes, large specimens of the larger species are often not preserved because of their bulk. As a further complication the investigator is rarely certain whether size is restricted by genetic factors, by environmental factors, or by both.¹

¹After these data had been summarized, word was received from Mr. Charles E. Shaw of the Zoological Society of San Diego advising us that the black specimen of *H. horridum* depicted in plate 8 had attained an over-all length of 800 mm. Also, Mr. Carl Kauffeld of the Staten Island Zoological Society has supplied us with a specimen of *H. h. horridum*, with an over-all length of 830 mm, after preservation. The original sources of these specimens are uncertain. On the basis of pattern and scutellation the lizard in San Diego is identifiable as *alvarezi* and possibly came from Chiapas. The other probably came from Colima. It is doubtful, of course, whether our small samples include specimens close to the maximum for all races

In figure 14 we have plotted the maximum adult sizes for lizards of both sexes in each of the subspecies, both over-all dimensions and snout-to-vent length. On this basis there is a gradual increase in size from *alvarezi* to *exasperatum*, with a reversal in the trend from *suspectum* to *cinctum*. It may be questioned whether the maximum size provides a satisfactory criterion, in view of the difficulties that collectors have in preserving large specimens.

We have therefore essayed other means of dealing with size. An examination of the gonads

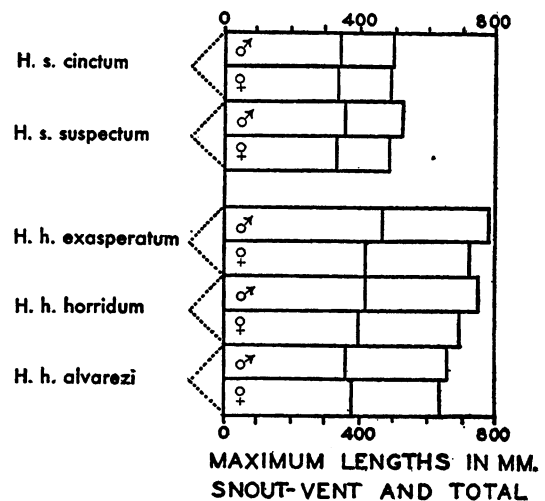


FIG. 14. Total lengths of maximum-sized specimens of each sex in samples representing the five subspecies of *Heloderma* (entire bar), and snout-to-vent lengths (vertical line within each bar) of the same individuals.

indicates that the testes as well as ovaries are smaller in immature individuals than they are in those assumed to be reproductively mature, and, further, the oviducts of sexually mature females are thickened and better developed than

of *horridum*. On the other hand it is conceivable that under suitable conditions in captivity an individual might reach larger dimensions than those attained by members of the same race in their natural habitat. We have found this to be true of some amphibians.

they are in immatures. Excluding immature specimens on this basis, we have calculated the mean snout-to-vent length of mature specimens in each sample, with the following results (means for males and females, respectively, follow the name of the subspecies): *alvarezi*, 320 and 340 mm.; *horridum*, 338 and 352 mm.; *exasperatum*, 354 and 352 mm.; *suspectum*, 292 and 289 mm.; *cinctum*, 300 and 308 mm. These data disclose a trend similar to but not identical with that based on verifiable maximums, with an increase in the size of adult males from *alvarezi* to *exasperatum*, followed by a sharp reduction in the size of *suspectum*. However, *cinctum* proves to be larger than *suspectum* on this basis. Similar trends are indicated for females, although the average size of those in the sample of *horridum* is slightly larger than those of *exasperatum*.

The data available are manifestly inadequate, although we are inclined to believe that the general trend within *horridum* is towards increasingly larger size towards the north, which suggests a correlation between size and mean wet-season temperatures. However, if *cinctum* does, on the average, attain greater dimensions than *suspectum*, as the analysis of our data for the sample suggests, it may be doubted whether this correlation exists in the races of *suspectum* unless maximum size proves to be a more reliable criterion.

PATTERN AND COLORATION

Descriptions of patterns, the variations observed, and the changes that take place during the ontogeny are provided in the taxonomic section of this paper. Reference to plate 13, which depicts adults of each of the five races, will serve to illustrate the general trend observable in the pattern and color. The darkest coloration occurs in the population at the extreme southeast, with a trend towards an increasingly lighter coloration in the populations to the north.

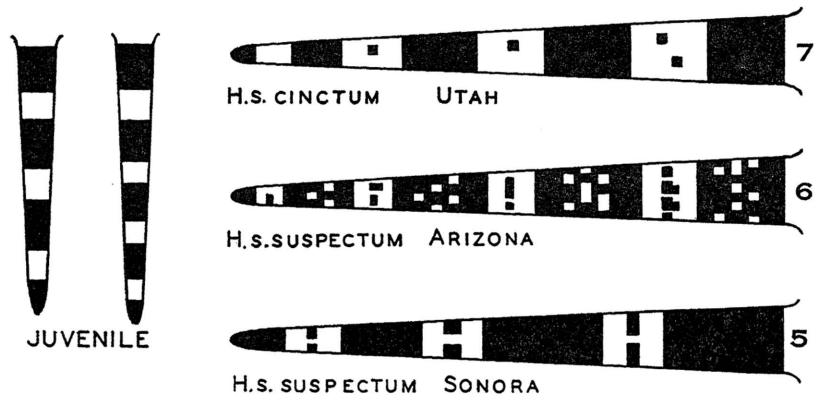
Owing to the variations and complexities of the pattern on the trunk of individual adults, we have not attempted to treat these characters in quantitative terms. However, by means of schematic diagrams (fig. 15) we have been able to illustrate the types or sorts of pattern that occur on the tail of lizards in our samples and to ascertain approximate percentages for

those occurring in the individual races (fig. 16). Also we have counted the number of black bands present on tails and interpret the data in terms of percentages (fig. 17). The information thus derived indicates the existence of similar trends in the races of each of the species, with a tendency towards patterns containing greater percentages of the lighter elements at the north, coupled with an increase in the number of dark tail bands, which are, however, narrower in the northernmost race of each species.

There is, therefore, an over-all trend from the simple, nearly uniform, black pattern in Chiapas towards one containing an increasingly larger percentage of the lighter color as one proceeds towards the northernmost population in Utah and Nevada. Aside from the fact that the Chiapan population inhabits a region with somewhat less rainfall than the average for the range of *horridum*, it would seem that something of a correlation exists between the general coloration and the precipitation, with the paler-colored animals inhabiting the more arid portions of the range. Unfortunately we have no data concerning the average relative humidity in the region inhabited by *alvarezi*, although it is described as being "quite humid," and we infer that it is a more humid region than most localities inhabited by *horridum* and *exasperatum* on the Pacific drainage of México.

Whereas the reptiles inhabiting desert regions are generally paler than those of more humid regions, there are notable exceptions to the rule among the Agamidae (Parker, 1935) and the Iguanidae (Klauber, 1939a), both families of which include relatively black lizards inhabiting desert areas. It is noteworthy that the black lizards more commonly inhabit rocky areas, where their black bodies are easily mistaken for crevices in the rock by some predators. Hence it is possible to interpret in terms of protective coloration the existence of both light and dark species in deserts. Others (Cowles and Bogert, 1944; Allee and Schmidt, 1951; as well as Parker and Klauber, cited above) have called attention to possible thermal implications of such colorations. Any interpretation at present is largely speculative. Whatever inferences one may draw, it is apparent that the phenomena observed in *Heloderma* conform to the principle of Gloger's rule, with

TAIL PATTERN TYPES IN HELODERMA SUSPECTUM



TAIL PATTERN TYPES IN HELODERMA HORRIDUM

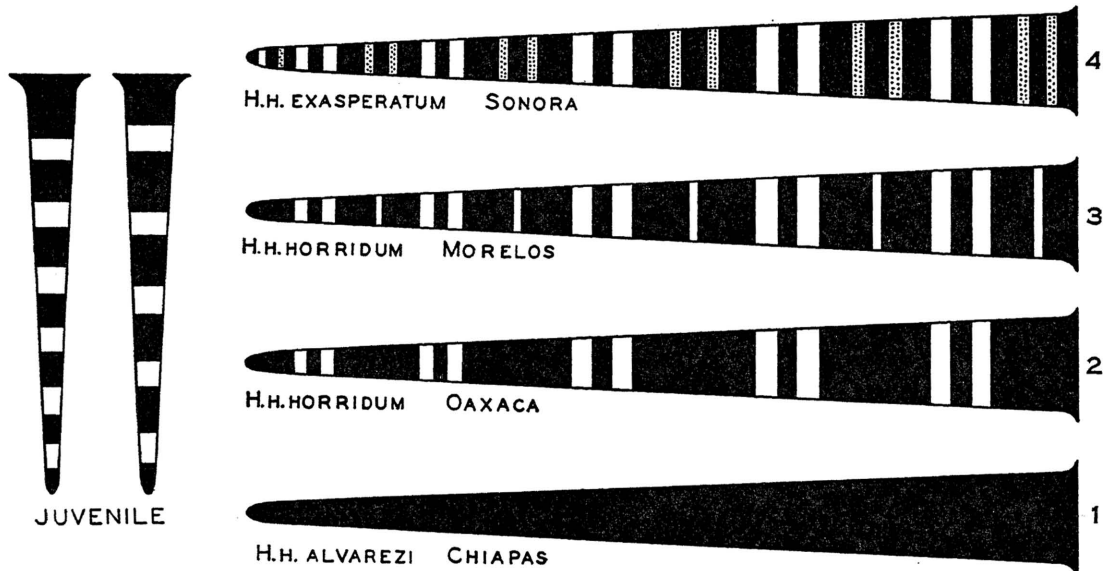


FIG. 15. Diagrammatic illustrations of patterns on the tails of adults and juveniles of subspecies recognized within the genus *Heloderma*, showing north-to-south trends (upper to lower).

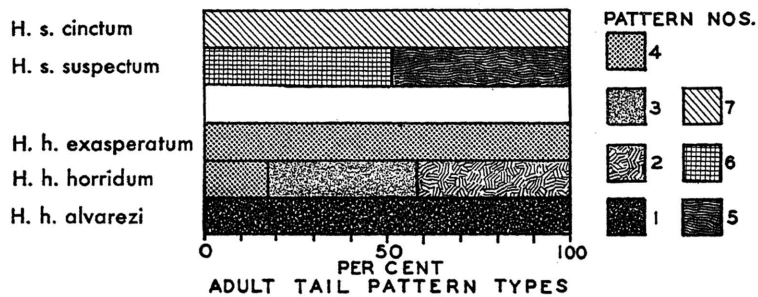


FIG. 16. Bar diagram showing percentages of tail pattern types (illustrated in fig. 15) in each subspecies of *Heloderma*.

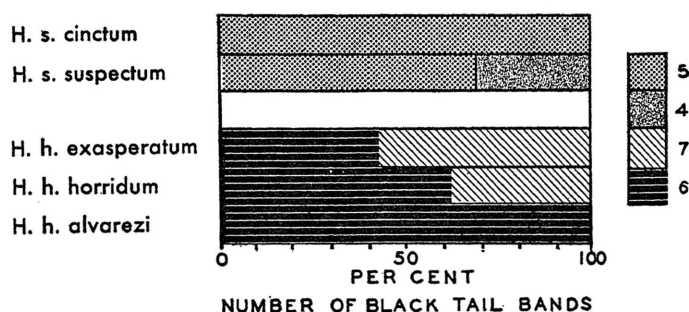


FIG. 17. Bar diagram showing percentages of samples representing subspecies of *Heloderma* having the number of black tail bands (or vestiges of them) indicated by the key to the right.

the darker populations inhabiting the damper regions, and the palest coloration present on individuals from the more arid portions of the range.

ONTOGENETIC CHANGES IN PATTERN

The clinal trend observed in the pattern of the adult also involves what is essentially a gradient in ontogenetic changes. The data available, while incomplete and not readily subject to quantitative analysis, indicate that, aside from the gradients that exist in the number of tail bands, juveniles of all three races of *horridum* are essentially similar in pattern and the juveniles of both races of *suspectum* are virtually indistinguishable. However, the most profound changes, from a pattern consisting of simple black rings on the tail and black saddles on the dorsum to a nearly uniformly black adult, occur in *alvarezi*. Towards the north increasing amounts of the juvenile pattern are discernible in the adult, until at the extreme north, *cinctum* as an adult retains virtually all the elements of the pattern seen in the hatchling, with relatively minor changes (see taxonomic section for descriptions of the changes that occur in each subspecies).

SCUTELLATION

Geographic trends in variation within one or both species are present in the majority of the 22 characters tabulated and graphed. Such characters as the number of preoculars and the number of canthals are subject to variation, but with such minor departures from the mean and such insignificant differences between the

racess and species as to suggest randomness. The same may be said for a third character, the number of lamellae on the under side of the fourth toe, although in each species there is a tendency towards an increase in the northernmost race. Nineteen other characters of the scutellation can be summarized under four headings, as follows:

A. Characters in which there is virtually a continuous trend from Chiapas northward: This situation exists for five characters: (1) the number of internasals (fig. 18), uniformly two in *alvarezi*, but with increases in the percentages having the alternate number of three in the samples from more northern populations culminating in *cinctum*, in which nearly one-fifth of the population is so characterized; (2) the number of pairs of infralabials in contact with the chin-shields (fig. 19), with a shift from two in *alvarezi* towards one in the populations towards the north, where all *cinctum* have but one, and with a sharp differ-

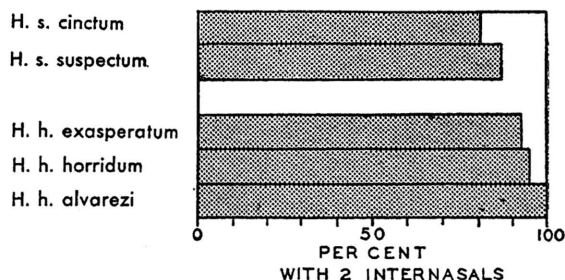


FIG. 18. Bar diagram showing percentages of each sample representing individual subspecies that have two internasals (instead of three).

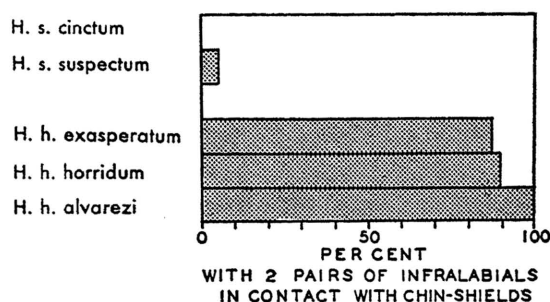


FIG. 19. Bar diagram showing percentages of each sample having two pairs of infralabials in contact with the anterior chin-shields.

ence between the frequencies of the two species; (3) the number of rows of scales around the midbody (fig. 20), with a fairly continuous increase from *alvarezi* to *cinctum*; (4) the number of scales down the midline of the head from the internasals to the occiput (fig. 20), with a trend from *alvarezi* with the fewest to *cinctum* with the most; and (5) the number of ventral scales from the gular fold to the vent or cloacal opening (fig. 21), with a more or less continuous increase in the means for the samples from Chiapas northward. Were it not for the fact that in each of the five characters the smaller species, *suspectum*, tends to have more scales than the larger one, it might be inferred that the higher number of scales was correlated with an increase in the adult

size. In view of the nature of the trends, it seems more probable that the increase is in some fashion associated with the progressively more arid habitats between Chiapas and the range of *cinctum*.

B. Characters in which there is a trend in the races of *horridum*, followed by a reversal of the trend at species level, and then a repetition of the same trend in the races of *suspectum*: Three characters fall into this category: (1) the number of interorbitals or the scales across the head between the superciliaries (fig. 22), with a marked increase from *alvarezi* to *exasperatum* (which, unlike the nominate race, is subject to no variation in the sample available), but with the mean for both races of *suspectum* falling closer to that for *H. h. horridum*; (2) the number of rows of subcaudals (fig. 23), which is obviously correlated with the differences between the species in proportional tail length and quite possibly with differences at the subspecific level as well; (3) the number of scales around the base of the tail (fig. 24), which shows a trend differing from that for the number of scales around midbody, with a sharp reversal at the species level. The latter two characters are possibly correlated with the relative tail length, whereas the number of scales across the head seems to be reflected in the proportionately broader head of *horridum* (see table 1), as well as the propor-

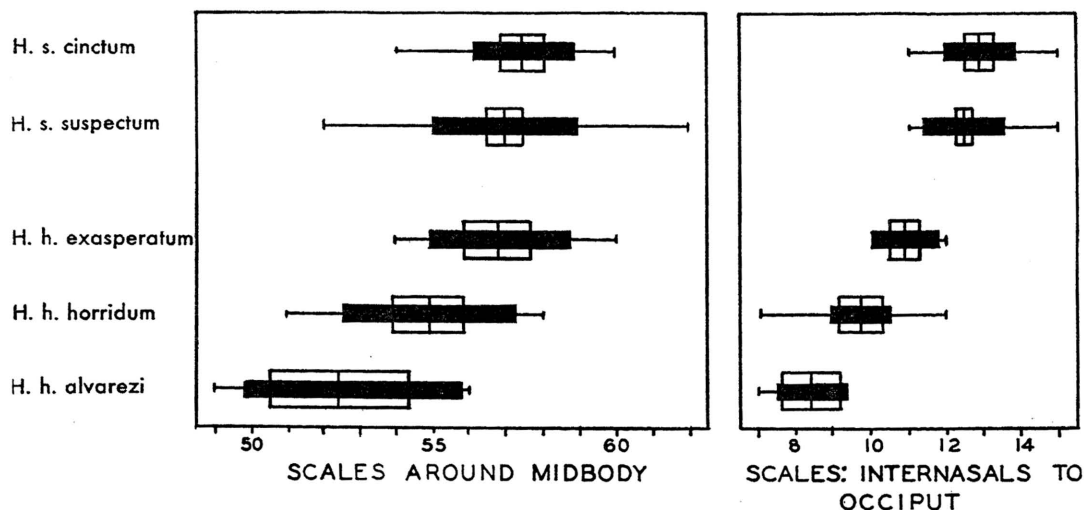


FIG. 20. Graphs showing trends in the number of scales around the midbody and showing trends in the number of scales between the internasals and the occiput.

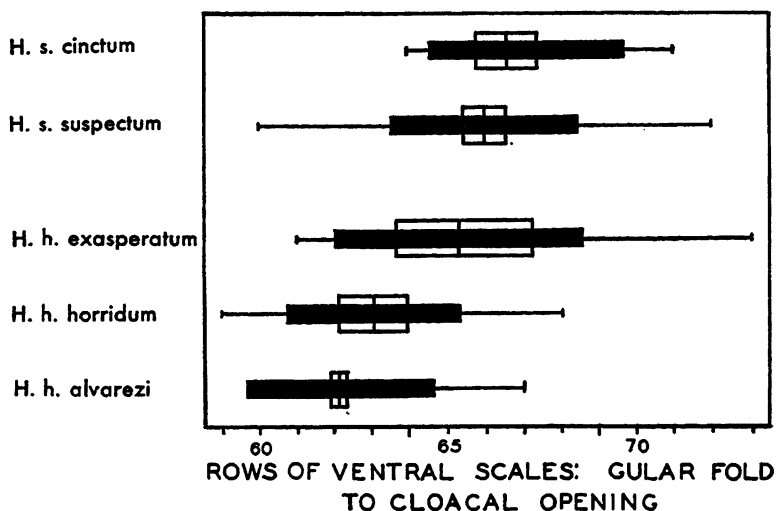


FIG. 21. Graph showing trends in the number of rows of ventral scales between the gular fold and the cloacal opening or vent.

tionately broader head of the northernmost race of each species. It is probably significant that each of the three characters in this category seems to be correlated with those of proportionality, quite unlike those in the previous category, where the trend continues without reversal at the species level. There is no obvious correlation of such trends with a trend for any single factor of the environment. But it may be noteworthy that the reversal in the trend for the three characters occurs at the species level. Unlike endotherms, which tend to have larger bodies in cool climates (Bergmann's rule), terrestrial ectothermic vertebrates tend to attain their maximum dimensions in warm climates. Thus it is not totally unexpected that *horridum* attains a larger size. In view of the fact that the growth of individual organs and structures is often a function of the growth of the whole organism, the relatively longer tail of *horridum* may possibly be ascribed to allometric growth. This seems to be borne out by the fact that juveniles of *horridum* and *suspectum* are approximately the same in snout-to-vent length (fig. 12), whereas the tail of *horridum* is proportionately longer. Moreover, as *horridum* increases in size there is a tendency towards an increase in proportionate tail length that exceeds that of *suspectum*. Thus the reversal in the trend for three scale characters is probably to be ascribed to the phenomena associated with allometric

growth, whereas the tendency towards a higher number of subcaudals and scales around the base of the tail in the northernmost population of each of the species seems to be associated with the increasing aridity of the climate towards the north. If an interaction of two factors be considered, the explanation for the increased number of scales at the north would seem to be the same as that indicated above for the characters in category A.

C. Characters in which there is a discernible trend in the races of *horridum*, but none in those of *suspectum*: Four characters fall into this category: (1) the shape of the mental scute (fig. 25), which varies from wedge-shaped in *alvarezi* through intermediate stages within the range of *horridum* to "shield-shaped," characteristic of all specimens of *exasperatum* examined, whereas in both races of *suspectum* the scute is wedge-shaped, much as it is in *alvarezi*; (2) the nature of the supranasal contact (fig. 26), almost uniformly with the postnasal in *exasperatum*, and in a very small percentage of the nominate race, but separated from the postnasal in all specimens of *alvarezi* and in both races of *suspectum*; (3) the number of postrostrals (fig. 27), the mean of which tends to increase slightly from the Chiapas population northward to *exasperatum*, with a tendency towards fewer in the races of *suspectum*; (4) the number of pairs of chinshields in contact (fig. 22), two more com-

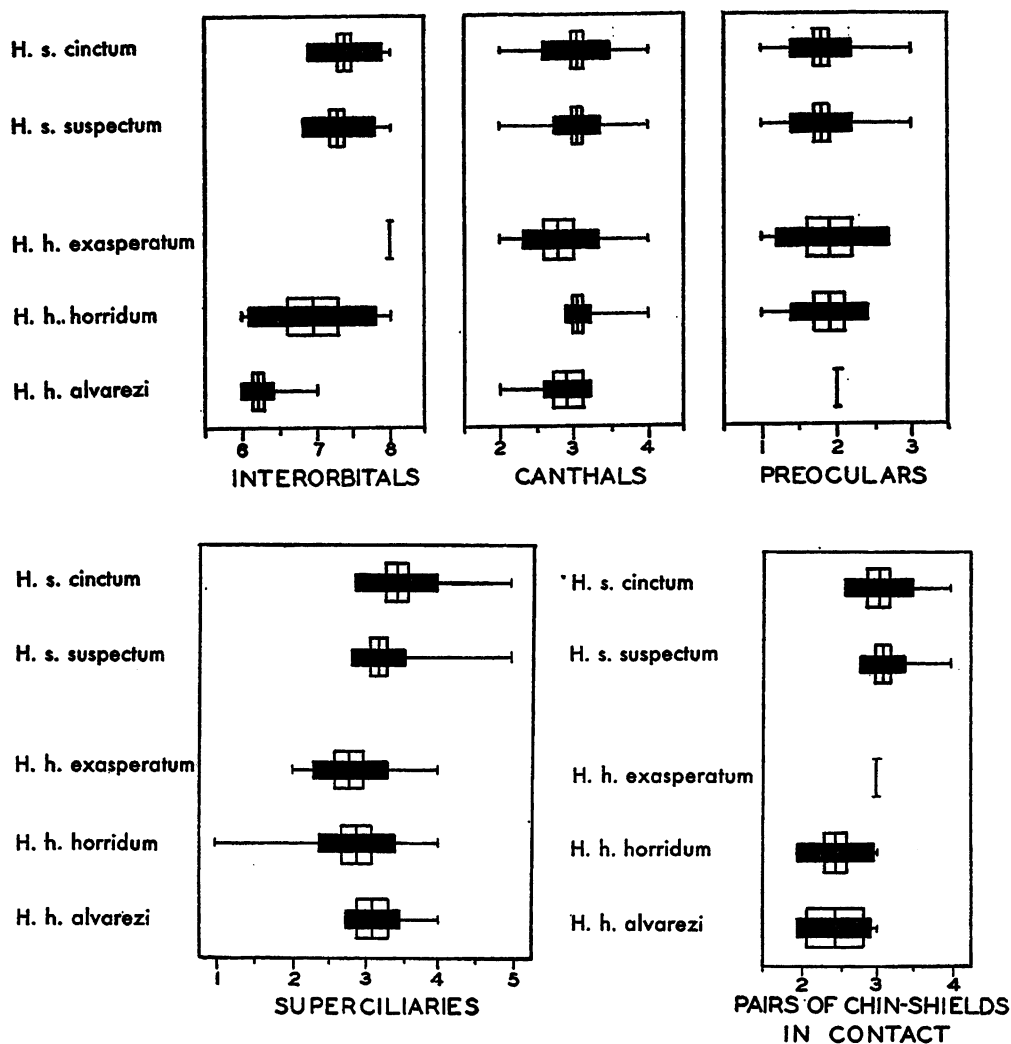


FIG. 22. Graphs showing trends in the numbers of interorbitals, canthals, preoculars, superciliaries, and the number of pairs of chin-shields (right and left elements of each pair) in contact.

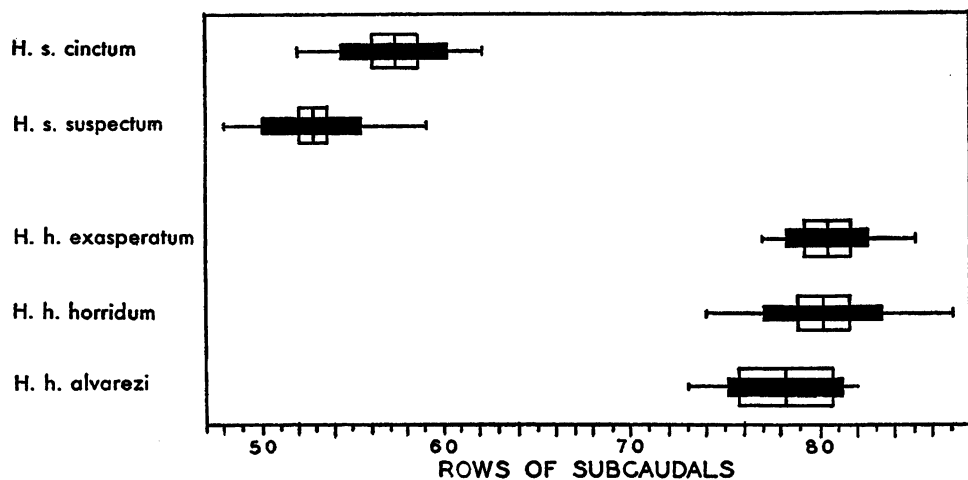


FIG. 23. Graph showing the trends, as well as the differences between the species, in the number of rows of subcaudal scales.

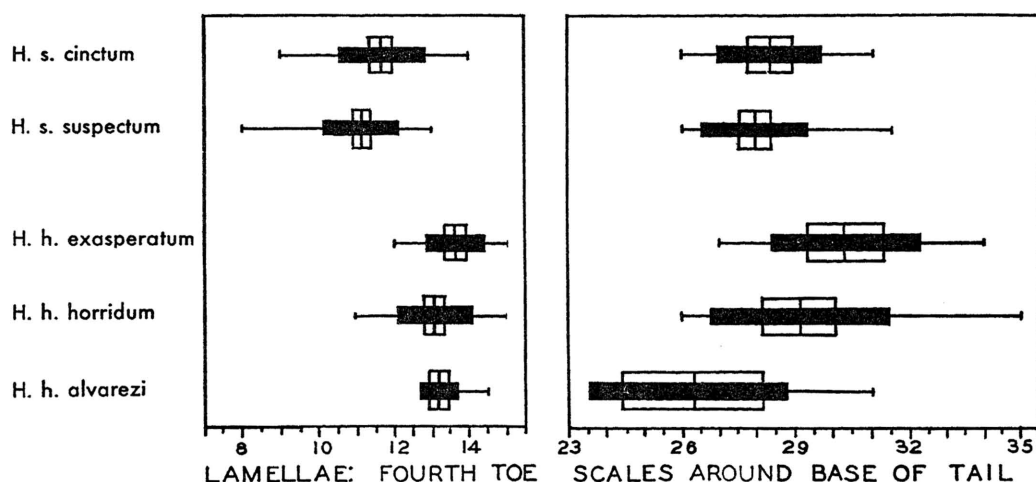


FIG. 24. Graphs showing the trends in the number of lamellae on the under side of the fourth toe and the number of scales around the base of the tail.

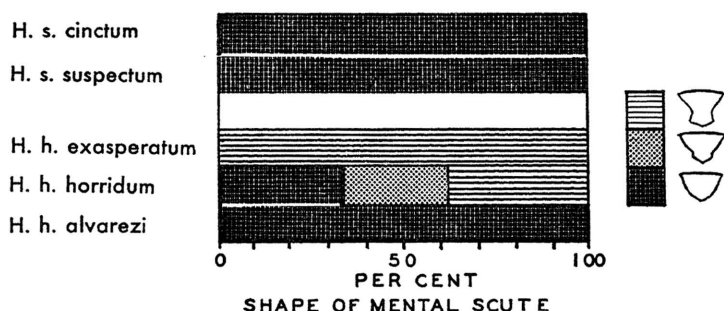


FIG. 25. Bar diagrams showing the percentages of each sample representing the various subspecies having the mental scute with the shape indicated at the right.

monly than three in *alvarezi* (which differs but little from *horridum*), but uniformly three in *exasperatum*, which more closely resembles the two races of *suspectum*, both of which occasionally have four.

The trivial nature of the majority of these characters makes it difficult to point out any significant correlations, although the fact that *alvarezi*, the smaller race of *horridum*, resembles the races of *suspectum* in the first three characters suggests the likelihood that these are associated with size. If so, changes in these characters from race to race may represent the pleiotropic effects of genes more directly associated with growth and size, and not the direct effect of environmental selection on the separate characters. It is difficult to offer

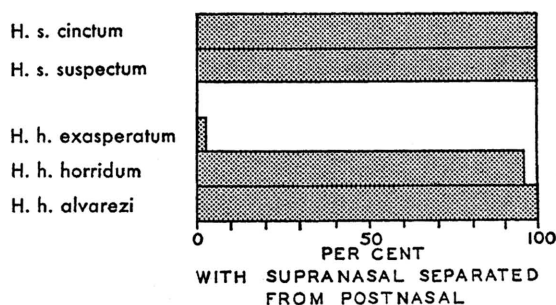


FIG. 26. Bar diagram showing the percentages of each sample having the supranasal separated from the postnasal rather than in contact as these two scales normally are in *Heloderma horridum exasperatum*.

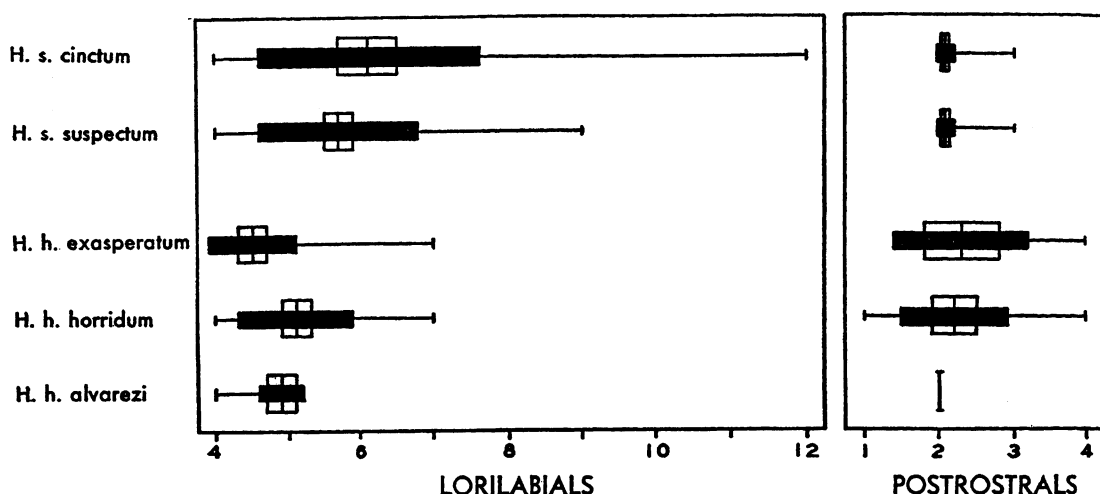


FIG. 27. Graph showing trends in the numbers of lorilabials and postrostrals.

any interpretation for the tendency towards an increased number of paired chin-shields in contact in the northernmost populations.

D. Characters in which there is a trend towards an increase, or less commonly a decrease, in the mean number of scales or in the frequency of occurrence of the character, followed by a reversal in the trend, usually at the species level: Characters in which such trends are discernible include the following: (1) the number of supralabials (fig. 28), probably correlated with (2) the number of infralabials (fig. 28); (3) the number of loreal scutes (fig. 28); (4) the number of lorilabials (fig. 27) in which the reversal lies between *horridum* and *exasperatum*; (5) the number of ventrals between the axilla and the groin (fig. 28); and (6) the number of superciliaries (fig. 22) in which there is a tendency towards a decrease from south to north in the races of *horridum*, followed by an increase in the races of *suspectum*. In addition (7) there is a trend (fig. 29) observable in the percentages in which the second supralabial is in contact with the nasal or prenasal (see fig. 30) of each sample, with a reversal at the species level. Scales in the lorilabial series are essentially upper portions of the anterior supralabials, and the failure of the second supralabial to extend to the nasal or prenasal may be interpreted as the result of the fact that the second supralabial has become divided so that the upper portion is counted as a lorilabial. The lorilabial, therefore, reaches

the nasal or prenasal instead of the second supralabial. Thus the decrease in the number of lorilabials in *exasperatum* (fig. 27) seems to be partly correlated with the undivided second supralabial present in all available specimens of this race. But for the fact that *exasperatum* tends to deviate from the trend, there is a general increase in the number of lorilabials, accompanied by an increase in the amount of variation, which is most extensive in *cinctum*. The nature of these variations suggests that the character has not been subject to great selective pressure and that *exasperatum*, perhaps fortuitously, has retained what is possibly the more primitive condition.

Except for the opposite trends in the number of superciliaries, the number of lorilabials, and the character of the supralabial contact associated with it, the trends are towards an increase in the number of scales towards the north in the races of *horridum*, with a relatively slight decrease towards the north in the means for those of *suspectum*. The majority of the trends thus parallel those for wet-season temperatures. It does not follow, of course, that a close correlation exists, nor is it certain that the similarity in trends necessarily reflects any association of cause and effect. The nature of the data does not permit us to do more than point to the possibility that the number of scales is affected by thermal factors.

In discussions of the characters that show a more or less steady trend from south to north

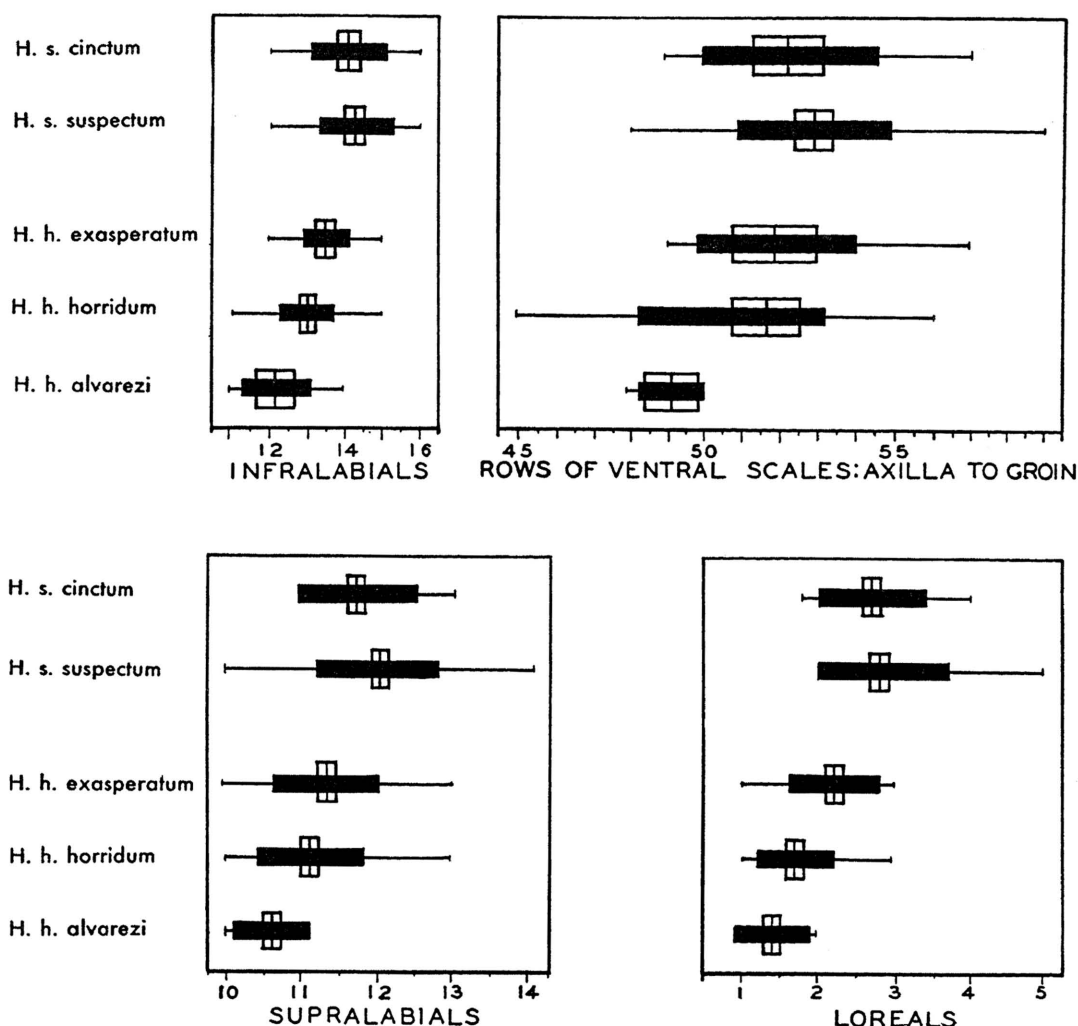


FIG. 28. Graphs showing trends in the number of infralabials, the number of rows of scales between the axilla and the groin, and the numbers of supralabials and loreals.

towards an increase in the number of scales, we have suggested that such gradients are associated with the progressive aridity towards the north. We are now suggesting that higher temperatures within the habitats occupied by some races of *Heloderma* produce similar effects. Our inferences are not readily subject to proof or disproof by experiment; such circumstantial evidence as we can assemble is necessarily open to question. Klauber (1941a) encountered similar problems in his interpretation of the results obtained from a study of the snakes inhabiting both the coastal and desert portions of San Diego County, California. He

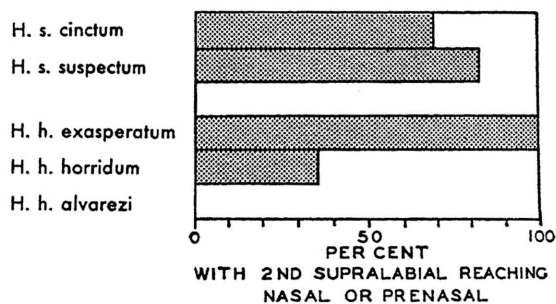


FIG. 29. Bar diagram showing percentages of samples representing individual subspecies having the second supralabial reaching the nasal or prenasal.

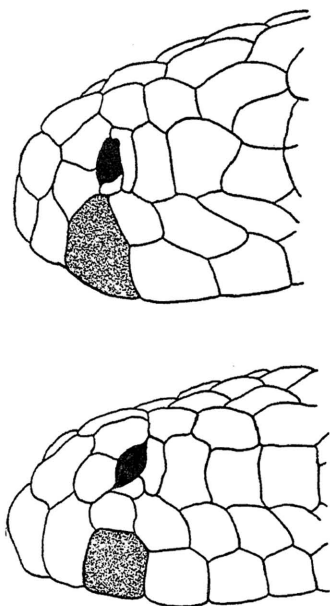


FIG. 30. Diagrams of the snout, illustrating second supralabial in contact with the nasal (upper) and separated from it as the result of the presence of a lorilabial (lower).

shows that there was an almost universal tendency towards a higher number of ventral scales in the snakes from the desert region as opposed to those of the same species from the more humid coastal region. However, he is careful to point out that, while the difference in humidity is outstanding, the increase in the number of ventrals in the snakes on the desert slope might be attributed to other factors of the environment, notably temperature.

Clines have been reported in ventral counts for a number of species of snakes. As early as 1919 Van Denburgh and Slevin observed that in snakes of the genus *Pituophis* "the warmer and dryer the climate of a given locality the greater the number of gastrosteges [ventrals]." In a more recent study of the snakes in the same genus Klauber (1947) states that in the subspecies *P. catenifer deserticola* there is a decrease in the number of ventrals "from the Mojave Desert in California northward through Nevada to a low in eastern Oregon and Washington" that is possibly associated with a decrease in the temperature. Grobman (1941) notes that the southwestern race of *Opheodrys vernalis* has a greater number of ventrals than the race inhabiting the north-

eastern portion of the United States.

Data are available for a few species of snakes inhabiting portions of the same region occupied by *Heloderma* on the west coast of México. Klauber (1941b) records data for two races of *Rhinocheilus lecontei*, *antoni* with a range that extends from Nayarit to northern Sonora having fewer ventrals and caudals than *R. l. clarus* to the north. Oliver (1948) reports that "there appears to be a clinal trend towards an increase in the number of ventrals from south to north" in *Thalerophis diplotropis*, a snake that ranges along the coast of México from Oaxaca to southern Sonora. Ortenburger's (1928) data (based on an extremely small sample) may indicate an increase in the mean number of ventrals in the racer, *Masticophis bilineatus*, from 191 in Oaxaca and 194 in Sinaloa, to 201 in Sonora, but with a drop to 200 in Arizona. A similar trend in ventral counts is noted by Bogert and Oliver (1945) for other species on the west coast of México; in *Hypsiglena ochrorhyncha* there is a trend in males from 163.3 in the states south of Sonora to 174.8 in the southern portion of the latter state, and again with a drop to 172.0 in Arizona, with a similar trend in females of 171.6, 178.0, and 180.6 for the respective regions. In *Oxybelis aeneus*, with a range that extends from southern Arizona to Brazil, there is an increase from 184.8 for South America to a mean of 187.9 for Central America that rises to 197.0 for southern Sonora.

Adequate material is available for relatively few species, but increases in the number of ventrals from south to north or from the foothills to the desert lowlands are indicated by Bogert and Oliver for snakes of the genera *Leptotyphlops*, *Phyllorhynchus*, *Thamnophis*, and *Salvadora* (see also Bogert, 1945). There is some indication of an opposite trend, that is, towards fewer ventrals at the north in relatively few species, notably in *Crotalus* and *Agkistrodon* mentioned by these authors. It is evident from other data, notably those supplied by Conant (1946) for snakes of the genus *Diadophis*, that trends towards higher ventral counts in warmer or more arid regions are not universal among snakes. Conant's data indicate a higher mean for ventral counts in the populations above the fall line of New Jersey and Pennsylvania, with low counts in the lowlands,

but with higher counts for the population inhabiting Long Island. As shown by Mertens (1934), high counts are commonly noted in insular populations. But the vast majority of the clines demonstrated for snakes indicate that higher ventral counts more often occur in the warmer, and frequently the drier, portions of the range.

Suitable data are available for few lizards inhabiting the same region as *Heloderma*. Bogert and Oliver (*supra cit.*) note that the southernmost population of *Callisaurus draconoides* in Sinaloa is characterized in part by having fewer lamellae on the toes and "the Mazatlán specimens fit into a geographical gradient which involves a decrease in number from north to south." H. M. Smith (1939b) reports 29.8 as the mean number of dorsal scales in *Sceloporus clarki boulengeri*, a lizard with a range extending from Jalisco northward to southern Sonora, whereas the nominate race, which ranges northward into southern Arizona, has a mean of 31.8. Oliver (1943) shows that in Sonora there is an increase from south to north in the number of enlarged dorsal scales in the lizard *Uta ornata*. Data supplied by Shaw (1945) indicate a rise in the mean of 147.8 for the race (*townsendi*) of *Sauromalus obesus* inhabiting coastal Sonora to a mean of 159.4 for the ventral scales in the race *tumidus* inhabiting southwestern Arizona, and a further increase to 186.8 in *S. o. obesus* in the deserts to the north.

Possibly other examples might be cited

among lizards, but these, chosen at random, point to the existence of clinal phenomena similar to those existing in *Heloderma*. However they do not indicate whether humidity, temperature, or some other feature of the environment is the causal factor. Only snakes have been subject to experimental test. Fox (1948) maintained gravid garter snakes (*Thamnophis*) at low temperatures and reports that they produced young with significantly fewer scales in several series than those of the young produced by snakes maintained at higher temperatures.

Such evidence raises the question whether many differences in scale characters are genetic or ontogenetic in origin. It is possible that some of the differences observed between populations of *Heloderma* are the direct result of the mean temperatures to which the eggs are subjected during incubation. Lacking better evidence to the contrary for the lizards of this genus, we conclude that whether genetically controlled or otherwise, the clinal trends in scale characters are largely attributable to gradients in climatic factors, of which temperature and humidity are outstanding. We are inclined to assume that the majority of the characters are controlled primarily through genetic mechanisms (see also Mayr, 1948), and that while evolution has affected the organism as an integrated whole, the variations observed in individual populations reflect the response, through natural selection, of the populations to climatic differences.

BARRIERS AND DISCONTINUITIES

Aside from the taxonomic implications, it is of some interest to note where the major discontinuities occur in the clines in size, pattern, and scutellation. We have previously listed five characters not subject to clinal trends in either species, but which serve to distinguish the two. Of those that are clinal the major discontinuity, that is, the greatest difference between means for adjacent populations, occurs between: (1) *alvarezi* and *horridum* in four characters; (2) *horridum* and *exasperatum* in eight; (3) *exasperatum* and *suspectum*, and hence at the species level, in 14; and (4) *suspectum* and *cinctum* in only one character.

On this basis the northernmost population,

H. s. cinctum, in a region climatically somewhat different but without any apparent barrier between it and *suspectum* is, therefore, the most poorly differentiated. Second is *alvarezi*, separated from *horridum* only by a relatively low continental divide (elevation ca. 400 meters) over which there is possibly a continuous or partly continuous range and perhaps some gene flow. The range of the race *H. h. exasperatum*, as far as present records are concerned, is separated by a hiatus of approximately 200 miles from that of *H. h. horridum*, and it is considerably easier to define. Finally in the majority of the characters the major difference between means occurs at the species

level between *horridum* and *suspectum*, with a gap in the range of 150 miles¹ that probably is of less significance than the fact that there is a relatively abrupt change in environmental factors, as indicated by differences in the vegetation.

The complete geographical isolation of two populations almost certainly preceded the present differentiation, and were more known of the history of the group, it probably could be shown that isolation of two populations occurred long prior to Pleistocene times. In view of other evidence discussed by Bogert and Oliver (*supra cit.*), it is possible that *suspectum* and *horridum* both evolved from a common stock that became split when colder climates forced its retreat to the south, the stock that became *suspectum* being isolated on the peninsula of Baja California, while *horridum* descended from that on the mainland. Fossil evidence is lacking for Baja California, but because the extinct *H. matthewi* occurs in Oligocene deposits east of the present continental divide, it is not difficult to assume that lizards of the family were once far more widely distributed and possibly represented in California and Baja California. No one doubts that there have been extensive climatic changes, and relatively minor changes would account for the hypothesis suggested.

However, the semi-relict nature of the family, with its relatively limited distribution, makes it more than a little difficult to draw any inferences concerning the factors that led to the initial geographical isolation of the two stocks. Ecological factors may prevent any extensive overlap in their distributions under present conditions. The two species probably would not interbreed even though they were able to exist in the same habitat. In fact, a small overlap in range may eventually be

demonstrated. Bogert and Oliver (1945) mention nebulous reports of both species in the vicinity of the Río Fuerte in northern Sinaloa. It is in this region that an overlap in range would be expected if it actually occurs.

Wallace (1876) mentions the family "Helermidæ" as "Mexican only," a statement that is nearly correct. Schmidt (1946) and Clark (1952), following beliefs entertained by most herpetologists since Boulenger (1885), cite the occurrence of *Heloderma* in the American tropics and of *Lanthanotus* in Borneo as an example of discontinuous distribution of a family, Schmidt pointing out that it has a striking parallel in the distribution of tapirs. Dunn (1931), mentioning the same distribution as well as the occurrence of *Heloderma* in the northern Oligocene, doubts that these families can be "considered as 'Neotropical.'" Darlington (1948) who correctly notes that "it is a question how close the relationship [of *Heloderma* and *Lanthanotus*] really is," dissents, suggesting that most faunal elements now in temperate climates had their origins in the tropics.

The latter view may well be correct. Helodermatids probably pushed northward into what is now eastern Colorado when conditions there were more nearly like the moist tropics of the present time. The Gila monster, a species that is ill adapted for life in arid climates to the extent that it shuns direct sunlight and restricts its activities largely to the rainy season, may well have acquired the adaptations it possesses as the region it now occupies became increasingly arid. It probably evolved along with the flora, which Axelrod (1950) describes as derived from the major continental Tertiary Floras that occupied those areas. "As gradually expanding dry climate restricted the Tertiary Floras to moister regions marginal to the areas of desiccation, subhumid communities on their borders slowly expanded and through time have produced species adapted to successively dry climates." The Gila monster, restricted by thermal limitations, modified its habits to avoid desiccation and survived along with the plants that became adapted for subhumid climates.

¹ A specimen of *Heloderma s. suspectum* (F.A.S. No. 8073) from the coast of southern Sonora between Yavaros and Agiabampo was obtained too late during the summer of 1955 to be included on the maps. However, the record indicates that this species occurs within 50 miles of the nearest locality for *H. horridum exasperatum*. We are indebted to Dr. Frederick Shannon for the privilege of reporting this extension of the range.

FOOD AND FEEDING HABITS

AMONG THE VARIOUS WAYS of finding out what lizards eat, there are few that are practical as well as adequate. Observations made on captives do not provide reliable information, because it is manifest that foods available under natural conditions are rarely if ever offered to caged specimens. On the other hand, captives may accept foods not ordinarily encountered by the species. An examination of the contents of the digestive tract in specimens preserved shortly after capture affords the only reliable means of ascertaining the normal diet of most species, and even this method has its limitations in some instances. When such liquid substances as the contents of eggs are devoured, it is difficult to estimate their bulk or even to identify their source unless a well-developed embryo is present or fragments of shells have been ingested.

Furthermore, lizards as large as those in the family Helodermatidae are not infrequently eviscerated by collectors faced with the necessity of obtaining properly hardened specimens with limited supplies of preservative.

The following account of the food and feeding habits of the *escorpión* and the Gila monster is not entirely adequate, as we have been forced to rely in part on information previously published. Few authors indicate the basis for their statements, which in some instances are little more than supposition. We have not attempted to quote from all the accounts that have appeared in popular articles, as most of these have been drawn from other sources cited. Our own observations supplement the review of the literature, and the conclusions summarized ignore statements unsupported by evidence.

DIET OF *HELODERMA HORRIDUM*

PREVIOUS RECORDS

Sumichrast (1864a) published the first account of the feeding habits of *H. horridum*. His paper, in French, appeared in a Swiss journal, and later the same year an English translation (Sumichrast, 1864b) was published in a British journal. Sumichrast states that, "As might be expected from the constraint and slowness of its movements, the *Heloderma* [*horridum*] can only attack an easy prey. Its food consists essentially of apterous insects, earthworms, myriapods, and small species of Batrachia, and sometimes even putrefying animal matters. It is fond of the eggs of Iguanas; it is not unusual to meet with it roaming about near the holes dug in the sand, in which these eggs have been left to the action of the rays of the sun." Later the same author (Sumichrast, 1869) supplied virtually the identical information, this time in Spanish, and published in México. Sumichrast's account, in part, was quoted by Bocourt in 1875, and requoted by Duméril, Bocourt, and Mocquard in 1878 (1870-1909).

Sumichrast does not indicate whether his information is based on hearsay evidence obtained from natives, from personal observation of the reptile's habits, or from an examination

of stomach contents. Nonetheless his statements have been widely and uncritically repeated, by Hoffmann (1890) for example, and later by many others. Garman's (1883) statement that lizards of the genus are "carnivorous," and "not at all particular as to kind and condition of food" probably is an inference from Sumichrast's 1864 account. After keeping a specimen of *H. suspectum*, Garman (1891) had good reason to modify such views. Duncan (1884) says only that *H. horridum* "prefers flesh to vegetables."

Gadow (1901), who thought that the differences between the two species were "rather imaginary," supplies a general account for both, and states that the "'Gila Monster' . . . crawls about in the evening in search of worms, centipedes, frogs, and the eggs of large lizards." Sokolowsky (1912) and later Werner (1913) repeat essentially the same information, crediting Sumichrast, but not making it plain whether they are discussing *horridum* or *suspectum*. Gilmore (1928) repeats Gadow almost word for word. Krumbiegel (1949) lists earthworms, chopped meat, small mice, frogs, and cockroaches as the food of *Heloderma*, presumably of both species. It may be inferred that this statement is based partly on supposition, there

being no conclusive evidence that earthworms, cockroaches, or frogs are ever eaten by either species.

Cuesta Terrón (1930) appears to be somewhat more cautious, noting that there is no certainty concerning the food of *horridum* in the wild. Observing that some authors state that the food consists of ants while others believe that it consists of the eggs of birds and reptiles, Cuesta Terrón suggests that the latter assumption is probably correct in view of the fact that captive specimens manifest a predilection for eggs and a complete indifference for insects and their larvae. Although Cuesta Terrón was describing the habits of *horridum*, his statements, in Spanish, are virtually translations of Ditmars' (1907) statements concerning *H. suspectum*.

Only two reports are based definitely on an examination of stomach contents. Bogert and Oliver (1945) report their findings for specimens taken at Alamos, Sonora, and quote Hilton, who examined the stomach contents of a specimen, now a paratype of *H. horridum exasperatum*, taken at Guirocoba in the same state. Hilton found what he believed to be the eggs of the Douglas quail (*Lophortyx douglasi bensoni*). The three specimens from Alamos examined prior to preservation contained white shell fragments and a yellowish liquid assumed to be the contents of eggs, probably those of one or more of the local species of doves. From Guirocoba specimens Zweifel and Norris (1955) report 13 eggs resembling those of quail in one *H. h. exasperatum*, and a nestling bird identified as a squirrel cuckoo (*Piaya cayana*) in another.

Señor Miguel Alvarez del Toro, who obtained most of the specimens of *H. h. alvarezi* now available, informs us (*in litt.*) that "For food they like rats, lizards and eggs. In captivity, like other members of the genus, they feed on raw eggs and chopped meat."

ANALYSIS OF CONTENTS OF STOMACHS AND INTESTINES

To obtain more reliable information concerning the food habits of *H. horridum*, we have examined the digestive tracts of all suitably preserved specimens at our disposal. Less than half of the specimens available were usable for the examination of stomach contents. Some had been eviscerated; others (the three Alamos

specimens that originally contained the remains of eggs, for example) had the stomach contents removed prior to preservation. Some, including five of the paratypes of *H. h. alvarezi*, were known to have been retained in captivity prior to preservation and hence may have contained food not ordinarily encountered under natural conditions. The remaining specimens, totaling only 21, were assumed to have been preserved soon after capture. No marked differences between the subspecies are indicated, and the information below summarizes the data derived from representatives of all three.

Of the 21 digestive tracts examined, four were virtually empty, containing only a few grains of sand. Two contained small amounts of unidentifiable material and fragments of plants. Food material was present in the stomachs of but six of the remaining 15 specimens, although the other nine had identifiable remains in the lower intestine. The data obtained are inadequate for a meaningful quantitative analysis. However, a qualitative analysis of the contents of the 15 digestive tracts discloses the following facts:

1. Mammal remains occurred in five. In all but one instance these consisted solely of hair, not readily identifiable. The exception, a specimen from Chilpancingo, Guerrero, contained partly digested feet and the pelvic region of juvenile mammals identified by Mr. George Goodwin as a cottontail (*Sylvilagus*) and a cotton rat (*Sigmodon*).

2. Birds were represented in six, by fragments of eggshells in five, and in one by feathers otherwise unidentified. The feathers occurred in a specimen of *H. h. alvarezi* from Cintalapa, Chiapas, that also contained a large grain of corn. The smallest specimen examined, a juvenile only 205 mm. in total length, contained fragments of eggshell, suggesting that the feeding habits of the young do not differ from those of adults. It is possible that all shell fragments are not avian, inasmuch as the eggs of a few turtles have hard, calcareous shell, partly digested fragments of which would not readily be distinguished from those of bird eggs. In some instances the eggs had been swallowed whole and not broken. The grain of corn presumably was ingested accidentally, or it may represent the undigested contents of the bird's intestinal tract.

3. Reptile eggs were identified as such in only two instances. The first, a *Heloderma* taken at Cerro de Mixtequilla near Tehuantepec, contained 35 leathery-shelled eggs, believed to be those of a lizard; a few of them were still undigested so that an approximate measurement of 23 by 13 mm. could be obtained of their leathery shell. The undigested eggs had not been chewed and presumably were swallowed whole. A rough pebble some 5 mm. in diameter was found in the same stomach, along with a few leaves. In the second instance a foot and portions of the carapace of an embryonic turtle belonging to the genus *Kinosternon*, together with the fragments of the eggshell that presumably had surrounded the advanced embryo, were found in the stomach of a specimen taken by James Peters near Sulatillo (La Placita) in Michoacán.

4. Insect fragments, mostly the elytra of small beetles or portions of flies, occurred in six digestive tracts, one of which also contained a mite. There is no reason to believe that any of the insects found were "intentionally" ingested by the lizard. It seems much more probable that the insects were attracted to the food being consumed by the *Heloderma*, or inadvertently were crawling on the eggs or the mammals being eaten. Dr. Mont A. Cazier identified beetles entangled in the white eggshells removed from the stomach of a Sonora specimen as those of a scarabid, *Canthon viridis*, a beetle that feeds on dung and one likely to be found in the nest of a bird. It is not impossible that some of the other insect fragments found in stomachs or intestines represent the undigested remains from the stomachs of juvenile birds that had been swallowed.

The eggs or fledglings of birds represent the

food most commonly eaten by *Heloderma horridum*. If we add the data for four specimens containing eggs reported by Bogert and Oliver, 10 specimens, or approximately 53 per cent of the 19 for which data are available, had devoured avian eggs or fledglings. Mammals occurred in but six, or 32 per cent, whereas reptile eggs were contained in but 11 per cent of the 19 individuals. Insects occurred in six (or 32%) of the stomachs, but they, as are the pebble, the grain of corn, the leaves, and the sand, are assumed to have been ingested accidentally while the mammals and the avian or reptile eggs with which they were associated in the digestive tract were being devoured. In some instances they may represent vestiges of the less readily digestible stomach contents of juvenile birds or other animals upon which the lizard preyed.

To summarize the results of our investigation, it is probable that birds' eggs or fledglings are eaten more frequently than juvenile mammals, and that reptile eggs, at least those of lizards and turtles, comprise an important but an even smaller proportion of the diet of *Heloderma horridum*. There is no positive evidence to confirm Sumichrast's statement that *H. horridum* preys on earthworms, myriapods, or amphibians. However, with reference to carrion, which Sumichrast also mentions, it would be difficult to ascertain whether animals found in the stomach had been dead for any prolonged period before they were eaten. As noted below, captive specimens of *H. s. suspectum* can readily be induced to devour dead mammals and birds, and as the food habits of the two species are apparently similar, we are inclined to believe that carrion may be eaten by *H. horridum*.

DIET OF *HELODERMA SUSPECTUM*

PREVIOUS RECORDS

The evidence thus far published suggests that the feeding habits of *H. horridum* are not appreciably different from those of *suspectum*. Prior to the turn of the century it seems to have been well known (Garman, 1890; Shufeldt, 1882, 1887, 1890) that *suspectum* could be maintained alive on a diet of eggs, although

Shufeldt (1887) reports that in London "one was induced to swallow a small rat," later (1891c) noting that "this reptile in nature often catches and eats small mammals and birds." Garman offered "insects, worms, young birds, mice, meats, and cooked foods," none of which was accepted voluntarily, even though occasional offerings put in the mouth were swal-

lowed. Cope (1900) is somewhat more explicit, observing that "like most of the individuals kept in confinement it [a specimen of *suspectum*] ate readily of raw eggs, lapping them up with the protrusible smooth extremity of the tongue," adding that Gila monsters "also drink water by inserting the nose into the fluid." It remained for Hylander (1954) to make the erroneous statement that the Gila monster "sucks" out the contents of the brittle shells of birds' eggs. Barbour (1926, 1934) says that both species of *Heloderma* "apparently feed largely upon birds' eggs," presumably basing the statement on earlier reports. Snow (1906) mentions a Gila monster that lived for three years on a diet of raw eggs. Brimley (1905) observes that a caged *suspectum* ate the eggs of domestic fowl "one every three or four days," but Woodson (1943a) says that the "diet in captivity is a beaten-up egg served once a week if the Gila monster is 12 or so inches in length and twice a week if it is 16 inches or more." With more precise data, Durham (1951) reports that a half-grown captive ate 27 eggs in 52 days during the summer, but later in the fall consumed only five eggs during a period of 39 days, and refused food after October 14. Eggs containing living embyros were eaten; excessively stale eggs were refused.

Ditmars (1904) states that captives could be induced to eat nothing but eggs, boiled, raw, or mixed with chopped meat. He notes that young rodents, grubs, meal worms, and ants were refused. In 1907 (and again in 1936, with minor changes) he observes that the "Gila Monster shows a decided liking for the eggs of fowls and reptiles and likewise decided indifference for insects and their larvae." By 1910 he includes rodents among the foods eaten, as noted below. Corle (1951) says of the Gila monster that "its food consists of mice, rats and insects," and that "it is a scavenger of sorts," but he does not state the basis for his assumptions. Dodge (1947) apparently was the source of statements subsequently published. He writes that the food of the Gila monster "consists chiefly of bird and reptile eggs, young rodents, and such small or juvenile creatures as it is able to catch." Conant (1944) says the Gila monster's food includes "small animals of any kind it can catch, plus the eggs of birds and reptiles." Klots (1954) makes a similar

statement, adding that the lizard "has despoiled many a nest of the Desert Quail, and other ground-nesters."

Several authors, Jaeger (1950) for example, continued to state that insects and centipedes are included in the Gila monster's diet. Hegner (1935) and Angel (1942) include ants. Lydekker (1913) lists "worms, frogs, centipedes, and iguanas' eggs." Sachs (1948) gives insects, worms, and frogs. Anonymous (1879) writes that "its food is such small reptiles, mice, crickets, and other insects that it can easily capture." Such statements are probably traceable to Sumichrast and the numerous authors who quote from his early account. Fahr (1912) did feed cockroaches to a captive specimen, but the insects had been mixed with raw egg. Snedigar (1939) and Woodson (1948), like many others who got their information from Ditmars' accounts, report that captives have been fed on a mixture of egg and hamburger. Woodbury (1933) notes that the niche of *H. suspectum* [*cinctum*] in Utah is not fully known, but he speculates, presumably from his observation of captive specimens, that it feeds on the eggs of birds or reptiles or perhaps the young.

As early as 1897 (1897a) Van Denburgh had stated of *H. suspectum* that "in spite of its clumsy form it sometimes climbs bushes probably in search of birds' eggs, which together with young rabbits, etc., form its food." By 1922 Van Denburgh had modified the latter part of this statement somewhat to include rodents (instead of rabbits), as well as reptile eggs, presumably taking into account the report by Ditmars (1910) that the eggs of snakes were "gulped down entire," by captive specimens. Ditmars notes further that "One Gila Monster consumed, in rapid succession, eight eggs of a Chicken Snake."

Kauffeld (1943) makes the categorical claim that "certainly in captivity no other food than eggs is accepted" by Gila monsters, even though Shufeldt (1887, 1891d), as noted above, had mentioned a rat devoured by one, and suggested that under natural conditions they caught small mammals and birds. Kauffeld (1954) emended his earlier statement, reporting other lizards, mice, and carrion to be included in the diet of *H. suspectum*. Earlier (1949) he had reported circumstantial evidence of one feeding on the

carcass of a dead jack rabbit, of finding rabbit hair and a shell from a snake's egg in the feces. The feces of a second specimen contained rabbit hair and "several lizard egg shells." Ditmars (1910) had observed that these lizards "sometimes take mice, catching the animals by a quick turn of the head as they run by; the prey is shaken for a moment, then held in a tight grip in an evident wait for the venom to do its work." In our experience, as described below, the Gila monster is incapable of catching active, adult rodents, whereas small mice, rats, and hamsters are killed and devoured without any delay that might have permitted the venom to act. Kohlhaas (1941) mentions that a captive specimen bit a mouse and suggests that Gila monsters may feed on juvenile rodents and other foods.

Roberta D. Ortenburger (1924) reports finding the foot and part of the leg of a large lizard (*Cnemidophorus*), unidentified ants, small Diptera, and bits of grass (*Bouteloua*) in the digestive tract of *H. suspectum* [*suspectum*], the grass being presumed to have been seized accidentally. She adds that Gila monsters "also eat the eggs of Gambel's partridge and possibly those of other ground-nesting birds." The same information with minor discrepancies is reported by Ortenburger and Ortenburger (1926), along with additional comments concerning captive specimens that ate the eggs of domestic fowl, "in all cases breaking the egg from the side and eating the contents, none being wasted." A year later Netting (1927), apparently unaware of the papers by the Ortenburgers, makes the guarded statement that the Gila monster "probably eats the eggs of ground-nesting birds." Woodson (1944), who apparently obtained his information from published sources, states that in its native state the Gila monster "feeds largely on bird eggs, small rodents, and lizards."

No one appears to have doubted that eggs are included in the natural diet of the Gila monster. Arrington (1930) quotes Vorhies as having found a "small furred mammal in the stomach of a newly captured *H. suspectum*," and adds that an amateur herpetologist reported three new-born jack rabbits in another's stomach. Arrington, however, could find "nothing to substantiate these views." Mice and young sparrows that he placed in a cage with eight

suspectum remained for a week without being molested. Six years later Vorhies (1936) writes that the food of the Gila monster consists of "some smaller lizards, small mammals (rodents), and to some extent the eggs or young of birds when available."

The inclusion of fledgling birds in the diet of *suspectum* remains to be substantiated. However, the statements by Vorhies and the amateur herpetologist concerning mammals in the diet that Arrington doubted can now be considered verified. Hensley (1949) states that immediately following its capture a *Heloderma* taken in southwestern Pima County, Arizona, disgorged three cottontails (*Sylvilagus auduboni arizonae*). He adds that a border patrolman in the same region saw one of the lizards regurgitate a young nestling cottontail when the lizard was attacked by a dog. Further confirmation is provided by Shaw (1948) who examined the stomach contents of 15 *H. suspectum*. He found only two containing food, probably because many specimens had been kept in captivity prior to preservation. In one there was a young roundtail ground squirrel (*Citellus tereticaudus*) and the unruptured leathery shells of nine otherwise unidentified reptile eggs, as well as fragments of a blossom presumed to have been ingested accidentally. The second contained remnants of the same species of ground squirrel. Shaw adds that a captive Gila monster is known to have eaten an adult collared lizard (*Crotaphytus collaris*). There still seems to be little justification for the statement by H. W. Parker (1944) that the food "consists chiefly of small lizards," or the comment by Burton (1949) that both species feed "largely on lizards."

Woodson (1949b) has published a summary of the food habits of *Heloderma*, but it is not clear whether he is referring to one or to both species. He notes that of 41 sources that list the food of these lizards, "in the native state," only five or six indicate that the report was based on personal observation. Many of the statements included in Woodson's summary evidently were based on earlier published reports or possibly mere supposition. Thus little importance can be attached to the fact that the eggs of birds were mentioned most frequently, followed by small mammals, lizard eggs, including those deposited by *Heloderma* itself,

insects ("including grubs, crickets, and ants"), snake eggs, and other lizards. A few of the sources mentioned earthworms, toads, centipedes, and live snakes. Woodson adds that one person makes the categorical statement that *Heloderma* "subsists on carrion."

Commenting on the results of his survey, Woodson observes that under the conditions in captivity the food of *Heloderma* "consists of whatever it can be induced to consume," noting that some captive individuals accept food stubbornly refused by others. Woodson, somewhat ambiguously, also provides a list of "other rations" said to include such doubtful items as dry bread and bone meal. Captives may have been induced to consume such foods if they are mixed with egg, although such details are omitted. Woodson concludes his account with the statement that "turtle and other reptilian eggs, mice and small snakes have been fed" to captive lizards of the genus *Heloderma*, but that "none has proved as beneficial as the raw eggs of the barnyard fowl." No other author has indicated that small snakes are preyed upon, and the reliability of the original source for the statement is to be questioned. It may have been based on the observation that, when confined in the same small cage, a snake may be seized or bitten by a disturbed Gila monster, as Ditmars (1907) and Woodbury (1928) note. This, of course, is a defensive reaction, and while snakes may be killed under such conditions, they are not eaten.

More recently Stahnke (1950) has endeavored to summarize the information concerning the feeding habits of *H. suspectum*. He describes how a captive specimen attacked and devoured a young rabbit, and quotes Evans, a taxidermist said to have examined "many stomachs" of Gila monsters, finding that the majority of them contained the eggs of quail or other ground-nesting birds. In some cases the smaller eggs had been swallowed whole. According to Stahnke, Evans had also observed very young chipmunks and rabbits in the stomach contents. Still later Stahnke (1952) reports that a Gila monster disgorged two juvenile ground squirrels (*Citellus tereticaudus arizonae*), the same rodent that Shaw (*supra cit.*) discovered in two other specimens. Stahnke comments on the astonishing bulk of the squirrels as compared with the size of the lizard

that had devoured them.

The swallowing of quail eggs without breakage had previously been reported by Arnberger (1948), who tells how a Gila monster disgorged nine eggs identified as those of the Gambel quail (*Lophortyx g. gambeli*). Several years previously (the date is not recorded) Herbert Brown sent two eggs (now U.S.N.M. No. 15865) of the Gambel quail to the United States National Museum, noting that they had been "swallowed and disgorged" by a specimen of *suspectum* taken near Tucson.

Stahnke (1950) also mentions finding shriveled eggs approximately the size of those belonging to the same species of quail in the feces of a Gila monster, adding that they may have been those of the desert tortoise *Gopherus agassizi*. Hensley (1950), with uncertain but far more convincing evidence, has tentatively identified the two eggs found in the stomach of a Gila monster as being those of the tortoise.

Although Ortenburger (*supra cit.*) had reported insects in the stomach of *suspectum*, Stahnke observes that "we have no positive evidence that the Gila Monster will eat either insects or their larvae." Insects are certainly ingested, but it is to be doubted that they are eaten intentionally.

SUPPLEMENTARY DATA

No series of preserved specimens of *H. suspectum* suitable for an examination of their stomach contents has been available. However, observations made on captive Gila monsters, one of which was kept over a period of 14 years, provide additional data that supplement those reported by others.

We are primarily concerned here with the nature of the foods consumed. Sensory cues utilized by Gila monsters to distinguish between edible and inedible substances, as well as those used to locate food, are discussed in an ensuing section of the paper.

An adult *H. s. suspectum* taken on the outskirts of Tucson, Arizona, in April, 1938, lived for over 13 years on a diet that consisted solely of eggs, including those of pigeons and those of the domestic fowl. However, when this same Gila monster was offered a dead bird, a rather large fledgling of the domestic pigeon, it took it readily and swallowed it whole. Later this lizard was readily induced to eat raw horse

flesh cut into squares of suitable size and placed in front of the reptile. Sometimes the meat was taken directly from the forceps. Contrary to published accounts, we did not find it necessary to mix horse meat with egg in order to induce the lizard to eat it.

Juvenile hamsters (*Cricetus auratus*), whether alive or dead, were eaten by Gila monsters. Similarly juvenile albino mice and rats of semi-domesticated strains were taken either dead or alive, although if alive and large enough to be active the rodents easily escaped the lizards' jaws.

Gila monsters kept in zoological gardens have sometimes been provided with special diets. Mr. Roger Conant of the Philadelphia Zoological Garden informs us that both species of *Heloderma* have been supplied with a mixture consisting of the following: raw ground horse meat, 55 to 60 per cent; raw ground carrots, 8 to 10 per cent; cod liver oil, 0.5 per cent; oyster-shell flour, 0.5 per cent; with the remaining 30 to 35 per cent made up of what is called "mixture No. 1, which is roughly comparable to any good brand of dog meal."

This mixture was varied considerably from year to year, particularly during World War II, when some of the ingredients were difficult to obtain. Mr. Conant adds that very often a quantity of the mixture was placed in the bottom of a shallow pan, with one or two eggs broken over the mixture and partially mixed into it. The pan was then placed in a cage and several lizards, both *horridum* and *suspectum*, would be moved up in position, with their heads facing the dish. Almost immediately they would start lapping up the egg, and then continue to eat the mixture. A specimen of *H. horridum* survived for nine years on this diet, thereby establishing a longevity record for the species in captivity.

SUMMARY

From the information in the sources given above, it is evident that under natural conditions the following foods are included in the diet of *Heloderma suspectum*:

1. Juvenile mammals, including roundtail ground squirrels (*Citellus tereticaudus*), cottontails (*Sylvilagus auduboni*), and probably jack rabbits (*Lepus*, either *californicus* or *alleni*, possibly both).

2. Eggs of ground-nesting birds, including those of the Gambel quail (*Lophortyx g. gambeli*), which may be swallowed whole, without breaking the shell. Thus far there is no evidence that fledglings are eaten by *suspectum*.

3. The eggs of reptiles, possibly but not certainly including those of the desert tortoise (*Gopherus agassizi*), and, rarely, adult lizards (*Cnemidophorus* sp.).

Insects, including ants and flies, grass, blossoms, and doubtless other small bits of debris are accidentally ingested, but these are not to be considered part of the normal diet. The small rodents may have been dead when found and eaten by Gila monsters, but there is no evidence that carcasses of larger mammals provide sources of food, except for Kauffeld's (1949) report of one found with blood on its lips that seemingly had been feeding on the carcass of a jack rabbit.

Despite the lack of precision in the statement of Evans, quoted by Stahnke (1950), there is no reason to doubt that the eggs of quail or ground-nesting birds comprise a major portion of the diet. It is possible that there are regional or seasonal differences in feeding habits, and in view of the miscellaneous foods that have been taken by captive specimens it is probable that Gila monsters are even more catholic in their diet than the available information would indicate.

The feeding habits of *horridum* closely parallel those of *suspectum*. Little importance can be attached to the fact that fledgling birds have not been detected in the normal diet of *suspectum*, or that lizards were not found in the stomachs of *horridum*. Juvenile rodents, lagomorphs, and the eggs of birds and reptiles are undoubtedly eaten by both species. Thus far there is no certain evidence that eggs are removed from avian nests when these are situated in bushes, as Van Denburgh (1922) suggests.

While in captivity Gila monsters have been induced to take the eggs of chickens, pigeons, turtles, lizards, and snakes. The eggs of fowl may be either cooked or raw and need not be fresh, although "excessively stale" eggs are rejected. *Heloderma suspectum* may even devour its own eggs. Rats, mice, hamsters, and young rabbits have been devoured whole, as have dead birds. Horse meat, both with and without egg,

has proved acceptable and so has hamburger. Cockroaches mixed with raw egg have been fed to the Gila monster, but otherwise there is no satisfactory evidence that insects, worms, centipedes, frogs, toads, or live snakes are ever voluntarily eaten. Gila monsters kept in a large vivarium at the American Museum of Natural History did not molest either toads or lizards,¹ of which several species of both were present, but it is evident from Shaw's statement (*supra cit.*) that on occasion a lizard may be attacked and eaten. Various mixtures of foods containing eggs are also acceptable.

Neither species of *Heloderma* is suitably adapted as a predator on ants, or on such other small insects as have been found in the lizards' stomach. Insectivorous lizards normally either seize their prey in their jaws, or else ensnare it on the sticky mucus-covered end of an extensible tongue. The broad snout and the heavy lower jaw of a *Heloderma* are scarcely suitable for the seizure of any but the larger insects, none of which is known to be included in its diet. The tongue is used to convey water or the contents of an egg into the mouth, but could not be used effectively to snare a small insect.

MEANS OF LOCATING FOOD

In view of the fact that the eggs of reptiles are exhumed and eaten by the Gila monster and its Mexican ally, it seems probable that these lizards employ senses other than vision in locating their food. Many reptiles, including some snakes, and most iguanids and agamids among the lizards, seem to be unaware of motionless objects and depend largely on the movements of small animals to detect their presence. It is more than doubtful that a lizard would be able to locate eggs so skillfully buried as those of lizards and turtles unless sensory mechanisms in addition to vision were brought into use.

From what is known of the habits and behavior of both species of *Heloderma* it may be inferred that these lizards utilize olfactory cues to locate and to distinguish their food. Kahmann (1932) was the first to suggest that the forked tongue of some lizards carried odorous particles to the organs of Jacobson in the roof of the mouth. Later Noble and Kumpf (1936) carried out experiments demonstrating that

some lizards, even when blindfolded, are able to locate hidden food by means of their olfactory organs alone. Their experiments indicate that the tongue-Jacobson's organ mechanism provides an important accessory organ of olfaction. Lizards with the tongue and Jacobson's organ intact were able to locate food more rapidly than those deprived of their tongues.

Although Noble and Kumpf carried out their experiments with a teiid (*Ameiva*), they cite earlier experiments that demonstrate the ability of a scincid to distinguish its eggs from those of other species by means of olfactory cues. However, only those lizards possessing the protrusible forked tongue were able to locate hidden food. In contrast some iguanids with all their sense organs intact and functional could never be induced to find hidden food.

Active lizards of the genus *Heloderma*, as do other anguimorphs as well as snakes, extend the tongue at intervals, the frequency depending in part upon their familiarity with their surroundings. Wevers (1910) observed that a captive *suspectum* spent much of its time moving about its cage, touching with its tongue everything that came within its reach. Observations carried out at the American Museum confirm this statement. Three *suspectum* that had occupied a small cage for several months were transferred to a larger one. The smallest, thinnest, and most recently captured of the three Gila monsters proved to be the most active. It moved about the cage, sometimes pausing but thrusting out its tongue at irregular intervals regardless of whether it was walking. During its greatest activity the tongue was

¹ This was true until the spring of 1953, when five collared lizards (*Crotaphytus collaris*) were devoured by Gila monsters obtained the previous summer near Tucson, Arizona. Several lizards, including three species of *Sceloporus*, one *Uromastix*, and the *Crotaphytus*, were in a large cage provided during the day with sources of radiant heat. The Gila monsters were more active at night, after the collared lizards had secreted themselves beneath rocks provided in the cage. Evidently the Gila monsters, which were abroad at night when lower temperatures prevailed, had dug the collared lizards from their places of hiding and eaten them. Diurnal lizards, immobilized by low temperatures that would be readily tolerated by *Heloderma suspectum*, could easily be preyed upon, as they manifestly were.

extended 46 times in the course of a minute. When a Gila monster is at rest and undisturbed, with the eyes closed, the tongue is no longer protruded.

Such observations are suggestive, but of course do not prove that the tongue is used to carry odorous particles to the organs of Jacobson, or that ordinary olfaction is involved in the location of food. However, the presence of reptile eggs in the stomachs of both *suspectum* and *horridum* strongly suggest the use of olfactory cues. Because the eggs of lizards, snakes, and turtles are ordinarily buried in the ground, a simple way to test the ability of Gila monsters to locate hidden foods consisted in placing the eggs of domestic fowl at various depths below the surface under conditions in which these lizards could reach them by digging.

MEANS OF LOCATING AND CONSUMING EGGS

Three Gila monsters, respectively 305, 310, and 320 mm. in snout-to-vent length, were available for this experiment. They were kept in a cage with glass sides with floor dimensions of approximately 3 by 1.4 meters, with sand and rocks on the bottom. One had been in captivity for over 12 years, and the other two had been obtained the previous summer. All were from Pima County, Arizona. None of these lizards had been fed since the previous fall. Throughout the winter they spent most of their time at rest in "burrows" excavated under pieces of slate that rested on larger rocks on top of the sand on the floor of the cage. Sources of radiant heat had been provided that would have enabled the reptiles to retain the body temperature within the range at which they are active at other seasons. The experiment was carried out during the month of April, when the lizards began to show signs of increasing activity.

At first the lizards were offered chicken eggs, placed on the surface of the sand. These were invariably broken from the side, as Ortenburger and Ortenburger (1926) indicate, in contrast to Ditmars (1907), who makes the erroneous statement that these lizards break a hole through one end of the shell. Considerable difficulty is often experienced in breaking the shell, even that of the pigeon's egg. Commonly the egg must be brought up against some object so that it is not pushed forward as the jaws are brought

to bear on it. Once the egg is broken open, however, the lizard easily employs its tongue to lap up the contents within the fractured shell. From time to time the head is raised to drain the accumulated liquid backward into the esophagus in much the same fashion as that employed by domestic fowl when drinking.

After the three lizards had been fed every other day for a week, an egg was buried approximately 3 cm. below the surface of the sand. Three days later it had been exhumed and eaten, with only a few fragments of shell left on the surface. The experiment was repeated at intervals, finally with the egg buried to a depth of 13 cm., where it rested on the bottom of the cage. Even though the eggs were as carefully concealed as possible and buried at different places each time, there was no evidence that the lizards experienced any difficulty in locating them. Sometimes they located the food within an hour or so, the amount of time required being more a matter of whether the lizards were active or otherwise. Although excavations were sometimes made beneath one of the rocks, it was evident that these were for purposes of concealment. There was no random digging; on the contrary, there was every indication that the lizards knew more or less precisely where the individual eggs were located beneath the surface.

On April 21, 1951, after all three of the lizards had become quite active, a fresh pigeon egg was placed in front of the two larger specimens. Each protruded its tongue, the tips of which were repeatedly brushed over the shell of the egg. After several thrusts of the tongue, one lizard raised its body and opened its jaws, which were brought to bear on the middle of the egg. The egg was pushed deeper into the sand but not broken. The lizard made further exploratory movements with its tongue and tried repeatedly to break the egg, finally succeeding in cracking it as it was forced against the tail of the second lizard. The latter lizard moved, and the egg was forced ahead of the more active lizard, which finally succeeded in breaking it when it was held in place against the edge of the cage. The less active lizard soon joined the other in lapping up the contents of the broken egg. Five minutes later virtually nothing was left except the larger fragments of the shell, some of the smaller ones having

been ingested along with the yolk and albumen.

At this juncture a second egg was placed in the cage, held momentarily in front of the more active Gila monster, and then moved along the ground *via* a circuitous path to a point approximately a meter distant. The lizard promptly began exploratory movements, with its neck arched and the snout directed downward towards the sand, as the tongue was repeatedly extended. It followed the course over which the egg had been moved for approximately half a meter, and then moved off to one side, evidently having lost the trail and become confused. After briefly wandering farther from the trail, it made a circle that brought it back across the course over which the egg had been moved. Here the lizard seemed once more to have picked up the scent, for it followed the course of the egg over the sand, but in the reverse direction so that it returned to the original position of the egg. Continuing onward, it moved to the vicinity of the other two Gila monsters, which were still lapping at the fragments of the first egg. It seemed probable that the odors emanating from the feeding site of the two other Gila monsters distracted the more active lizard in its efforts to locate the unbroken egg. The lizard paused to make excavations where some of the albumen had seeped out into the sand, and during the course of intermittent explorations it encountered the head of one of the less active animals, the snout of which had previously been thrust into the broken shell so that some of the contents of the egg adhered to it. The smaller Gila monster repeatedly pressed the tips of its tongue against the head of the other lizard, continuing this activity for a few seconds. Then the mouth was opened in an obvious effort to bite the larger Gila monster, which merely retreated a few inches and did not appear to be seriously disturbed.

In order to hasten the experiment the smaller lizard was picked up with forceps and moved back to the trail that had been rubbed in the sand with the pigeon egg. The Gila monster once more tried to follow the trail, moving first to one side of it and then to the other, as it progressed towards the egg farther ahead. Twice it came within 15 cm. or so of the egg, which it failed to locate, even though it was in plain sight on the surface of the sand. Re-

peatedly the lizard retraced its steps, crossing and recrossing the pathway of the egg, which remained undiscovered.

In view of the fact that the relatively large tongue is employed in lapping up liquid foods, it was doubted that its extirpation in some of the specimens would have given additional information of great value, even though it would have inhibited or prevented the lizard from using the tongue-Jacobson's organ mechanism to pick up olfactory cues.

From the nature of the exploratory movements, with the tongue repeatedly thrust out so that it came almost in contact with the sand over which the egg had been drawn, it seems probable that the tongue-Jacobson's organ plays an important role in the food-finding activities of helodermatids. On the other hand, the failure of the lizard to discover the egg even when it was only 15 cm. distant suggests that vision is not of great importance. However, vision may play a somewhat more important role when Gila monsters are preying upon juvenile rodents, as may be seen from the following account.

SEIZURE AND CONSUMPTION OF RODENTS

At 10:00 A.M. on May 17 two live juvenile Syrian hamsters (*Cricetus auratus*) approximately 80 mm. long and weighing 14 grams apiece were placed in the corner of a large cage. A Gila monster of moderate size, 305 mm. from snout to vent, was moved into position, with its head directed towards the hamsters at a distance of approximately 4 cm. A moment before, the lizard, with its eyes closed, had been basking beneath the rays of a heat lamp. Apparently it was awakened when seized by the forceps used to transfer it.

When placed in front of the hamsters, the Gila monster paused only a moment, then elevated the anterior portion of the body, opening its mouth with the head directed downward towards the hamster. Thereupon it moved rapidly, seizing the rodent at the middle of the body with sufficient force to crush it. (In subsequent feedings the rodent was often seized by the head; see pl. 15.) Almost immediately the reptile relaxed its grip as it maneuvered the lifeless rodent laterally, alternately seizing and relaxing its grip until the hamster's head was in the lizard's jaws. The rodent was drawn

back into the mouth by alternately lowering the snout and advancing the grip as the snout was raised. After three successive advances the body, including the short tail, had been drawn inside the mouth, which was then closed. Once more the head was bent downward, seemingly in an effort to assist the movements of the throat musculature as the rodent passed down the esophagus. The entire process required less than two minutes.

The second hamster was attacked almost immediately, but in this instance it was seized by the head, in somewhat the same fashion as shown in plates 15 and 16, where a slightly larger hamster was offered. Although the prey appeared to have been killed immediately, it was dropped momentarily and again seized by its head. The hamster was shaken violently when seized the second time, as though the lizard were avoiding the possibility of being bitten. Then the lizard, still holding its prey, turned around and moved rather rapidly along the edge of the cage, stopping approximately half a meter away, where it forced the posterior end of the hamster's body against the glass as it proceeded to engulf it. Once the rodent was inside the mouth, the lizard again lowered its snout (see pl. 16) as it had done previously after drawing the first rodent into its mouth. Both rodents had been swallowed in less than five minutes.

Forty minutes later, with a body temperature of 28.3° C., the same Gila monster was offered a half-grown white mouse weighing 14.9 grams. The rodent was promptly seized but managed to engage its teeth in the right lower lip of the lizard. Carrying the rodent, the Gila monster headed for the distant edge of the cage, making repeated efforts to better its grasp. Again using the glass to push against, it finally succeeded in getting the rodent into its mouth. The rodent was swallowed within four minutes after it was introduced into the cage.

A second mouse of similar size was introduced into the cage a few minutes later. It was readily pursued by the same Gila monster, which snapped at the mouse repeatedly as it nearly caught up with it. However, the mouse was much faster in its movements and the lizard never succeeded in grasping the rodent.

Later, while the photographs in plate 16 were being secured, the same Gila monster in

rapid succession consumed two hamsters with a total weight of 30 grams, and a white mouse weighing 15 grams, even though the lizard previously had been supplied with horse meat, eggs, and other food on alternate days. Prior to eating the rodents the Gila monster weighed 364 grams.

Virtually the same procedure was employed each time the lizard devoured a rodent. Although the time required varied somewhat with the size of the rodent, the engulfing process was essentially the same. Once the prey had been forced back into the esophagus, the lizard raised the fore part of its body, arching the pectoral region and lowering the snout as a means of temporarily shortening the neck. This action evidently serves to force the rodent downward into the digestive tract.

When a Gila monster is confronted with live prey its behavior is markedly different from that displayed by the same lizard in the presence of an egg. Dead birds, horse meat, and eggs are seized slowly and methodically, whereas when confronted by a live rodent, the Gila monster moves quickly, with an alertness rarely displayed under other conditions. When following the scent of an egg dragged over the sand, the lizard appears to be intent and alert, but it shows no sign of excitement when the egg is encountered. There is reason to believe, therefore, that helodermatids distinguish live prey from inanimate food.

A Gila monster was able to pick up and to follow the trail of a freshly killed mouse dragged over the sand, pausing to dig for a minute or so before losing interest. Olfaction undoubtedly plays some part in the recognition of juvenile rodents as suitable prey, and once stimulated by the presence of the small mammal, the lizard apparently makes use of its vision in pursuit and seizure. When a half-grown albino mouse weighing 24.8 grams was held with forceps in front of a Gila monster, it seized the rodent by the head. However, when the mouse was released from the forceps, it readily disengaged itself from the grasp of the lizard and fled. The Gila monster attempted to pursue the rodent, moving at a pace which, while rapid for the lizard, was no match for the speed of the mouse. Under these conditions the lizard did not rely upon its sense of smell to follow the course of the rodent. Although the

tongue was extended at intervals, and odorous particles were presumably picked up and carried to the organs of Jacobson, the lizard appeared to be depending more on vision in its efforts to locate the rodent. This was clearly indicated by the fact that when a black object (although the mouse was white) was waved outside the glass as the Gila monster crawled along the edge of the cage, the lizard's attention was immediately drawn towards the movement. With open mouth it approached the glass and tried repeatedly to bite the object, following its movements with precision as the object was shifted in position. Prior to having seized the mouse, the reptile was oblivious of such movements, but the seizure of the mouse seemingly provided the stimulus necessary to evoke further reactions as the result of visual stimuli.

As shown in the section on diet, juvenile rodents and lagomorphs provide important sources of food for both species of *Heloderma*. The size of the mammals eaten, as well as the account by Stahnke (1952) who had a half-grown Gila monster disgorge two juvenile ground squirrels of the same species, points to the probability that rodents and rabbits are seized in their nests. Such nestlings are unable to move with sufficient speed to escape the relatively clumsy and slow-moving reptile. There are no field observations to provide information concerning the behavior of the adult rodents that must often be present in the nest as the lizard approaches. However, the behavior of the Gila monster that seized a juvenile hamster and then fled from the immediate vicinity of the simulated nest in the laboratory suggests that this flight may be the normal means of avoiding attack by possibly aggressive parents of the prey. For the lizard would often be vulnerable while engaged in swallowing the small mammal, even though its venom apparatus could readily be brought into use were it attacked after the prey had been swallowed.

It is manifest that the crushing power of the jaws is sufficient to kill young mammals, which are devoured before the venom could possibly have time to act. Hence the primary function of

the venom apparatus would seem to lie in its use for defense, more especially because helodermatids are incapable of moving fast enough to escape many possible enemies or predators.

While further experimental evidence is needed to prove conclusively that helodermatids are capable of following trails with enough precision to lead them to their quarry, it seems altogether probable that olfactory cues are utilized by these lizards in their search for prey. It is doubtful whether nestling rodents could be found so often as they evidently must be were these lizards to rely entirely upon random hunting and their inferior vision. Odors left by parental rabbits and rodents going to and from the nest must provide clues that assist these lizards in finding its site once they are able to pick up the odorous trail leading to it.

Lizards of the genus *Heloderma* seem, therefore, to occupy a specialized niche not strictly comparable to that of any other saurian. In a few respects their feeding habits resemble those of some monitors (*Varanus*; see Cowles, 1930, for an account of *V. niloticus*), which devour the eggs and juveniles of both reptiles and birds, even though they are known to prey upon other animals. White (1952) records the destruction of nestling birds by *Varanus gouldi* in Australia. However, varanids are active, relatively swift-moving lizards, quite capable of pursuing small prey on the ground. In contrast, the prey of the slow-moving but venomous helodermatids is largely restricted to helpless nestlings, with this diet augmented by the eggs of birds and reptiles.

To summarize the present brief account, there is evidence for the belief that both vision and olfaction are employed to locate and to distinguish foods, with olfaction playing the major role in this activity. The Gila monster (and presumably the *escorpión* as well) behaves as though it distinguished live animals from carrion or eggs. Juvenile rodents are evidently killed by the crushing action of the powerful jaws rather than by the effects of the venom, which undoubtedly plays a part in the defensive activity of the lizards.

BODILY FUNCTIONS, BEHAVIOR, AND ACTIVITIES

FAT STORAGE, FASTING, AND FLUCTUATIONS IN BODY WEIGHT

THE MAJORITY OF ANIMALS living in arid regions must either be able to migrate or to tolerate prolonged periods of drought. Toleration of desert or semi-desert conditions entails not only the ability to survive without water but also the ability to survive without food for moderate periods. For where no surface moisture has been available for months or even years, few plants are able to bloom, and most sedentary animals are not abroad. Birds commonly migrate to other areas. Virtually the only larger animals seen abroad in areas where there has been no rain for long periods are in the neighborhood of springs. Along the western periphery of its range the Gila monster seems to be largely restricted to the vicinity of more or less permanent sources of water, and while it is probably absent from barren regions farther eastward, it undoubtedly inhabits extensive areas where surface moisture as well as food is virtually non-existent for long periods.

Even near the center of its range, *Heloderma s. suspectum* from time to time must be able to exist for months or even years with relatively little food or water. At Tucson, Arizona, for example, during a 30-year period the mean annual precipitation varied from 130 mm. (5.1 inches) to 611 mm. (24.1 inches). Farther west within the range of the species there is progressively less precipitation, with less than 125 mm. (ca. 5 inches) recorded as the mean annual rainfall for several stations in Yuma County, Arizona, not far west of the region where the Gila monster is known to occur.

In view of the fact that Gila monsters are not active during the colder winter months, the summer rainfall is of even greater significance. In extreme southwestern Arizona the average annual precipitation (United States Department of Agriculture, 1941, p. 720, map) during the 10 driest summers between 1899 and 1938 was less than 20 mm. (0.6 to 0.7 inches). Throughout much of the region inhabited by *suspectum* three or four consecutive years may occur during which precipitation is enough below the long-time average to produce conditions of drought. In such regions as Guaymas, on the Sonoran coast of México,

rain is likely to occur on only 23 days of the year, and there are years when scarcely any rain, or none at all, falls during the summer.

It is evident, therefore, that *H. suspectum* is adapted for an existence in regions where both food and water may be unavailable for relatively long periods of time. It is probable that this lizard can survive without food for two or three years, though data are not yet available to establish this assumption. It is doubtful whether the reptile can survive so long without water, however, which may account for the absence of the species west of the Colorado River, as suggested elsewhere.

FAT STORAGE

It has been realized for many years that there are fluctuations in the diameter of the tail in both species of *Heloderma*. Ditmars (1907), whose statement is the principal source for many comments by others, notes that the tail "acts as a reservoir for the storage of nourishment, when food cannot be obtained. . . . After a lizard of this genus has been feeding steadily, the tail becomes thick and round. A specimen with the caudal appendage in this condition can fast for some months without discomfort, but the tail steadily decreases in circumference. Thus it appears evident . . . that they experience difficulty at certain times of the year in procuring food." Arrington (1930) states that "The animal gorges itself to the utmost, and the surplus energy is actually stored in the bulky tail in the form of fat. Often on a barren year an individual will be found whose tail is noticeably small, with the skin on it shriveled and close set. With plenty of food the tail will fill out quite quickly, with a stuffed appearance, and often its circumference is almost doubled." To support his statement, Arrington depicts two specimens, one well nourished, the other not. Cochran (1943-1944), states that "when the lizard had been getting an abundance of food, the tail becomes swollen and heavy. In time of starvation, the tail shrinks decidedly, as the body of the lizard is nourished by the stored up fat." Bogert (1939) says that the Gila monster "stores sufficient energy as fat in

its tail so that it may be able to remain dormant in the cool depths of a burrow during the heat of summer."

While the last statement implies that fat is stored largely to enable the lizard to remain inactive during the periods of excessive heat, it should be noted that low temperatures also drive Gila monsters to cover under ground during the winter months. The thermal requirements and tolerances of the Gila monster are discussed in a separate section. It will suffice here to note that this lizard is more often abroad and active during the summer rainy season, and that the storage of fat is more aptly considered an adaptation for an environment subject to periodic droughts of longer duration than those of a seasonal nature.

After heavy rains in July of 1950, an adult female Gila monster was taken not far west of Quijotoa, Pima County, Arizona, in a region that had suffered from drought the previous three years. It was an extraordinarily emaciated specimen, with a slender tail. The bones in the pelvic region were conspicuously apparent beneath the skin in contrast to the rounded contours of Gila monsters taken in the vicinity of Tucson during the same period. In the laboratory cage the specimen from near Quijotoa consumed two eggs before retiring to an inactive state beneath a rock. It was not weighed and measured until April 25 of the following year, when it again became active. At this time it measured 300 mm. from snout to vent, with the tail 111 mm. long and 21 mm. in maximum diameter (see pl. 17, figs. 1 and 2). The specimen ate voraciously throughout the summer on a diet of rodents, horse meat, and avian eggs, and 197 days later the tail had increased over 59 per cent of its original width to a maximum diameter of 32.5 mm. However, there was no perceptible increase in length. Durham (1951) records a shrinkage of 20 per cent in the girth of the tail of a Gila monster during a 35-day period. No doubt exists, therefore, that there are extensive fluctuations in the bulk of the tail that are largely correlated with the availability of food and independent of growth.

Schneider (1941), who studied the gross anatomy of the tail, notes that there are extensive deposits of fat in the tail, with muscles, vertebrae, and connective tissue comprising a very small percentage of its bulk. In a large

adult, 52.5 cm. in over-all length, the greatest circumference of the body was 25 cm., while the circumference of the thickest portion of the tail was 16.5 cm. The whole animal weighed 1345 grams. With the skin, head, and feet removed, the remainder of the body weighed 725 grams, of which the tail alone comprised 115 grams. The fat in the freshly skinned specimen was yellow, felt greasy, and readily liquefied when heated slightly.

Cross sections of the tail show that the fat deposits are in four compartments, two above the level of the vertebrae, and two larger ones below, separated by narrow zones of muscle. With the skin removed, it can be seen that the fat deposits in the tail are made up of a series of symmetrically arranged lateral lobes so that the structure, to quote Schneider, "reminds one of a thick ear of corn." Towards the pointed terminus of the tail the lobes are not present, but anteriorly there are approximately 22 (11 pairs) of these "*Fettbehälter*," the largest of which is 2.5 cm. long and 1 cm. in width. Schneider does not mention the fact, but anteriorly the fat bodies extend from the tail into the coelomic cavity, the posterior portion of which may contain heavy accumulations of fat.

Schneider points out that similar but not so well-developed structures are present in the caudal appendage of the Australian stump-tailed lizard (*Trachysaurus* [now *Tiliqua*] *rugosus*). Similar structures are undoubtedly present in other lizards, notably in *Coleonyx variegatus*, which inhabits the deserts in the southwestern portion of the United States. This gekkonid, not unlike others in the deserts of Australia, Africa, and Asia, has a slender tail that rapidly increases in diameter when an abundance of food is supplied. Schneider suggests that such fat storage is comparable to that in the hump of the camel, in the tail of some sheep, or in the hump in other ungulates inhabiting arid steppe regions. Schneider concludes that such fat deposits provide nutritive as well as water storage.

The Schmidt-Neilsens (1952) point out, however, that there have been misunderstandings concerning the role of oxidative water and the mechanism by which it is formed. They note that water is formed only by the oxidation of hydrogen, in an amount equivalent to

the hydrogen oxidized. To quote them, "There is no obscure mechanism for the formation of additional 'metabolic' water as pictured by some authors. . . . The formation of oxidative water requires oxygen, and the necessary ventilation of the lungs involves the evaporation of water." The Schmidt-Neilsens compare the amounts of water formed when various foodstuffs are metabolized, noting that while fats have some advantages over proteins, in actuality there is little to support the belief that fat storage provides a source for an appreciable amount of oxidative water.

The Schmidt-Neilsens are more directly concerned with water metabolism and water conservation in desert mammals, which of course differ physiologically from the reptiles. Parenthetically they observe that "In cold blooded animals the conditions for evaporation are entirely different. Cold blooded animals do not appreciably heat the inspired air, and the lower the temperature the less water is necessary to saturate the air at that temperature. In a saturated atmosphere, the evaporation from a cold blooded animal is practically nil, but not completely so, because the body temperature of the cold blooded animal, due to its metabolism, is slightly higher than of the surroundings."

Under laboratory conditions, where reptiles are rarely provided with sources of heat that enable them to regulate the body temperature by behavioral means, their body may indeed be at approximately the same thermal level as their surroundings. However, under natural conditions, as noted by Bogert (1949a), many reptiles while abroad and active maintain the body at mean temperatures greatly exceeding those of the surrounding air. Under exceptional conditions at higher altitudes lizards in the Caucasus are reported by Strel'nikov (1944) to have the body temperature as much as 29° C. above that of the surrounding air. Pearson (1954) reports iguanids in the Andes with body temperatures 31° C. higher than the adjacent air.

Contrary to the Schmidt-Neilsens' assumption, therefore, it is manifest that lizards and other reptiles, particularly diurnal forms, do transfer heat as well as moisture to the inspired air, especially if they inhabit desert regions where the humidity is low. It has been observed by Cowles and Bogert (1944) that respiratory

cooling is commonly employed by reptiles as they approach the upper limit of their temperature tolerance. Because reptiles pant when exposed to direct sunlight in desert regions as an effective means of lowering their body temperature, it can scarcely be questioned that moisture is lost to the air expelled from the lungs. Despite the lack of morphological specialization in reptiles to assist in heating the inspired air, there can be little doubt that the formation of oxidative water would involve evaporation from the lungs, the use of which would be required to obtain the necessary oxygen.

It follows, therefore, that fat storage in the tail of the Gila monster cannot be considered an adaptation providing an important source of water during periods of drought. On the other hand, this fatty reserve is drawn upon, even when water is available under conditions of captivity. Hence the ability of the Gila monster to store fat in the tail seems correctly to be considered an adaptation providing the reptile with a means of surviving for prolonged periods without food. Water conservation in such lizards is achieved by other means, which are discussed below in the section dealing with ecological requirements.

FASTING

Gila monsters can survive for months without food. Whether or not they can do so for a period of years has not been ascertained with certainty; too few specimens have been kept under ideal conditions in captivity where they were allowed to fast for maximum periods of time. Durham (1951) reports a specimen that fed voraciously during the early months of captivity in the spring and summer, but after October refused food for approximately a year. Although an effort was made to feed it by force once during the fast the lizard was dead at the conclusion of the period. Durham suggests that the animal failed to survive because it could not assimilate food at body temperatures below normal summer heat. It seems more probable that the animal died from other causes, quite possibly from delayed effects of overheating, because in another section of his paper Durham notes that 20 days prior to the lizard's death it "suffered a near sunstroke." Durham concludes that "a well-fattened animal could withstand, without seriously detrimental results, a

full year of fasting."

Under natural conditions the Gila monster is rarely if ever encountered with the tail so heavily laden with fat as it becomes when the lizard is provided with ample food in captivity. On the other hand, field observations indicate that during periods of normal inactivity, whether during the winter when air and soil temperatures are too low or during periods of extreme heat or drought in the spring or summer, the Gila monster retreats underground. It is probable that rodent burrows provide shelter, but the depth below the surface where the lizard comes to rest has not been ascertained. It may safely be assumed that extremes of both heat and cold are normally avoided, for even during the warmest weather, temperatures within such burrows hardly exceed 30° C. (Vorhies, 1945), and commonly are even lower.

Quite evidently the Gila monster is able to endure average room temperatures both summer and winter, for the individual maintained for a period of nearly 14 years at the American Museum was not provided with any source of heat whereby it could regulate its body temperature until the last year of its life. Shortly after its capture in 1938 it was fed, but during the following year it was not fed at all. Thereafter it was continuously supplied with water, but fed only during the late spring and summer months, when approximately one egg per week was provided. Rarely were more than a dozen eggs consumed during a year. During the winter months it refused food, and after the first year none was offered from October until sometime the following spring. There were relatively minor fluctuations in the diameter of the tail, which never became so swollen in appearance as it does in individuals that consume large quantities of food.

From our observations on this one individual it is evident that fasting for at least half the year is not detrimental to a Gila monster. We suspect, but cannot prove, that under natural conditions, where the reptile can retire underground to somewhat lower temperatures than those available under captive conditions, fasts as long as three years are endured. This assumption is based largely on the emaciated specimen taken in western Pima County, Ari-

zona, where there had been virtually no rain for three years.

FLUCTUATIONS IN WEIGHT

The only published information bearing on changes in weight that accompany fasting or heavy consumption of food by the Gila monster is that supplied by Durham (*supra cit.*). It is uncertain, of course, whether the gains in weight for a captive approximate those of the lizard under natural conditions, where the reptile can seek temperatures lower than those on the surface by entering underground burrows. On the other hand, the lizard would be forced to utilize more of its energy in foraging activities than it would as a captive. However, Durham's data indicate that *Heloderma suspectum* is subject to extensive fluctuations in weight, probably as the result of various factors.

According to Durham, a Gila monster obtained on May 14 in the vicinity of Hermosillo, Sonora, weighed but 277 grams nine days after its capture. But 64 days later, after it had consumed 13 eggs of the domestic fowl aggregating 702 grams, it showed a net gain of 302 grams. In other words, the lizard more than doubled its weight within two months—with an increase of 109 per cent of its original weight. This indicates a gain in body weight of 1 gram for every 2.3 grams ingested. It seems probable, however, that the lizard had been desiccated prior to the first weighing. Colbert, Cowles, and Bogert (1946) report that an alligator lost approximately 20 per cent of its weight during a 24-hour period when kept at a temperature of about 37.5° C., with the relative humidity at 37 per cent. The Gila monster does not appear to be markedly resistant to desiccation, and Durham notes that the reptile was transported across the desert between Hermosillo and Los Angeles, California, without being supplied with either food or water during the nine days required for the trip. Furthermore, the stomach was probably empty when it was first weighed, but full when weighed the second time.

Later in the summer when the reptile was weighed a third time, on August 30, after having consumed 15 eggs (with a total weight of approximately 810 grams) during a 35-day

period, the animal showed a gain of only 43 grams, having consumed 18.8 grams of food for every gram that it increased in gross weight. (Durham indicates that the ratio was 1/19.2, but if his statement that the eggs averaged 54 grams is correct, the above ratio can be calculated.) When the reptile was weighed for the fourth time on September 23, having devoured but four eggs (216 grams) during the intervening period of 24 days, it showed a net gain of but 13 grams. Contrary to the calculations supplied by Durham, his data show an increase in weight of 1 gram for every 16.6 grams ingested.

Durham suggests that his data indicate variations in the ability of the animal "to utilize food at various seasons and during various stages of growth and fattening." While there may be some variability from season to season, the initial desiccation of the lizard used by Durham provides an erroneous notion of the normal increase in weight during the spring. Whatever factors may have been involved, Durham's data show that there was an increase in weight of 129 per cent during a period of 123 days. At the time of the animal's death over a year later, the animal had declined in weight to 338 grams, having lost approximately 91 per cent of the weight gained during the first five months of captivity.

Others have recorded changes in weight, but they have not attempted to record the weight of the food consumed by Gila monsters. If the data obtained were to have been satisfactorily interpreted, more elaborate techniques than those employed by Durham would have been required, as it is necessary to know the moisture content of the food supplied. Mr. Roger Conant has supplied us with information concerning a specimen kept in the Philadelphia Zoological Garden, where it was provided with the special diet previously described. The lizard was a relatively small specimen when first received, from 15 miles northwest of Lordsburg, New Mexico. It had been in captivity for some months before it was first weighed on May 31, 1951. Approximately 21 months later it showed an increase of from 385 grams to 489 grams, or a gain of 104 grams, 27 per cent of its initial weight. During the same period it showed an increase of 22 per cent in length, as

described in the section dealing with growth.

Through the courtesy of Mr. Charles A. Hewitt of Buena Park, California, we can report the increase in weight of an adult specimen maintained in captivity from March 28, 1938, until November 14, 1948, more than 10½ years. When first received the Gila monster weighed 680.4 grams. When last weighed it had increased to 2154.6 grams, with a net gain of 1474.2 grams, representing 216.6 per cent of its original weight. Thus during a period of 10 years, 7.5 months, there was an average gain of roughly 140 grams per year. As the increase in length was only 70 mm., most of the increment in bulk represents adipose tissue. Woodson (1948) depicts the specimen, an individual of maximum size.

In the laboratory at the American Museum of Natural History records were kept of the increments and losses in weight of three specimens confined to the same cage. One individual (No. 1) had been confined to a small cage for almost precisely 11 years before the weights of the three were first recorded in April, 1951. The other two had been obtained the previous summer, one (No. 2) from the vicinity of Tucson being relatively plump, whereas the other (No. 3) was taken near Quijotoa following rains on July 15, but in a region where there had been virtually no rain for the previous three years. The latter, as noted elsewhere, was extremely emaciated in appearance when captured. All three of these Gila monsters were provided with an abundance of food consisting of eggs, including those of the domestic fowl and pigeon, juvenile hamsters, and albino mice and rats. Later they received horse meat. None of these foods was refused by any of the three. The individual that had been in captivity for the previous 11 years on a diet of eggs devoured a slightly putrefied squab on one occasion. Similar food was not offered to the other two.

The three animals were maintained in a cage provided with sources of radiant heat at one end. Thus they were able to regulate their body temperature, as they could either bask under the heat lamps or retire to cooler portions of the cage. A pool of water in which they could submerge themselves was also provided. Shelter was constantly available under rocks partially

submerged in the sand that covered the bottom of the cage. The sand was moistened daily. Owing to the fact that nearly the same food was available to all three, no effort was made to record the amounts of food consumed by individual lizards. They were kept under the conditions described, primarily for the purpose of ascertaining the extent of the fluctuations and the precision with which the thermal level of the body could be maintained. It was apparent, however, that all three reptiles were not equally active and that they did not consume similar amounts of food. Variations in weight were recorded at infrequent intervals, and, as may be seen in the following table, differences between the individual lizards are extensive, despite the fact that all three were subjected to the same environmental conditions.

Weight on April 20, 1951, prior to feeding in spring
Weight on November 1, 1951
Percentage of increase during 184-day interval
Weight on March 27, 1952, after winter without food
Percentage of weight lost during winter (146 days)

might be less at lower temperatures and with less fluctuation in the relative humidity—conditions that might well prevail in an underground burrow in the desert but that were not supplied in the laboratory.

Few data are available for the larger species, *Heloderma horridum*, which inhabits regions in Mexico that are not ordinarily subject to the droughts that characterize the areas within the range of *H. suspectum*. Mr. Charles E. Shaw of the Zoological Society of San Diego informs us that specimens of *H. horridum* having a slender tail when received rarely thrive in captivity, whereas those with a proportionately thick tail are not so difficult to maintain in good condition. When large quantities of food have been ingested by *H. horridum*, the tail becomes

No. 1	No. 2	No. 3
671 g.	445 g.	364 g.
765 g.	450 g.	657 g.
14%	1%	80%
535 g.*	337 g.	462 g.
30%*	25%	30%

The records for No. 1 indicated by an asterisk were actually made on February 13, when the individual that had been in captivity for nearly 14 years was found dead. It may be added that No. 3, which had shown a much higher gain in weight than either of the others, died somewhat later in the summer. Dissection disclosed it to be a female with mature eggs in the oviducts.

From these limited data it may be surmised that increases in weight depend upon such divers factors as the amount of adipose tissue already present when a Gila monster emerges from its hibernation or estivation, the ripening of eggs, and probably other factors not so readily determined. Losses in weight in proportion to the maximum attained during the previous fall are more nearly uniform, suggesting that nearly one-third of the body weight may be lost during hibernation. However, the conditions provided in the laboratory cage probably did not closely approximate those of the natural environment. Unfortunately there is no precise information concerning the temperature or humidity within the winter retreats normally sought by Gila monsters under natural conditions. It seems probable that the loss in weight

laden with adipose tissue just as does that of *H. suspectum*. We have described a well-fed specimen in the San Antonio Zoological Garden that had over-all dimensions of 780 mm., with a tail 330 mm. in length that had a diameter of 76 mm.

In September, 1951, Dr. James A. Oliver turned over to us a specimen of *H. h. horridum* of unknown provenance that had refused all food offered to it in the New York Zoological Park. At the American Museum it was placed in the same cage with the Gila monsters where sources of radiant heat had been provided. The *escorpión* was already somewhat emaciated, weighing only 440 grams on September 27, although it had an over-all length of 560 mm. It was active at periodic intervals, but consistently refused all food offered and grew steadily thinner. Six months after it had been received it was weighed, on March 27, and found to have lost 148 grams, or 33.6 per cent of its weight, as of September 27. The percentage of weight lost is roughly comparable to that lost by the three *H. s. suspectum*, despite the fact that the latter had been fasting for a somewhat shorter period.

The regions inhabited by *H. horridum* are

neither so arid nor subject to such prolonged droughts as the areas occupied by *H. suspectum*. Consequently the ability of *horridum* to store proportionately more fat in its relatively longer tail appears anomalous. Natural selection appears to have favored the proportionately longer tail in *horridum* but for reasons that do not appear to be coupled with its fat-storage requirements.

To summarize the information available, it is evident that *H. suspectum* is able to survive in regions where it is subject to droughts that are seasonal as well as to those of longer duration. Fat stored in the tail provides a source of nourishment (but a doubtful and certainly minor source of water) that enables the lizard to fast for periods of at least a year and probably longer. Fluctuations in body weight under conditions that are perhaps exceptional and not necessarily encountered under natural conditions include increases up to 129 per cent, and losses as great as 91 per cent during a period of a year and a half. Captives that fasted dur-

ing the winter months after being well fed the previous summer lost approximately one-third of their body weight.

The storage of fat within the tail as well as in the coelomic cavity by lizards of the genus *Heloderma* is believed to be an adaptation that enables such reptiles to survive in regions subject to periodic drought. Such specialized fat storage is not encountered in other desert-dwelling lizards, notably agamids and iguanids. The fact that it does exist in some scincids (*Tiliqua*), gekkonids (*Coleonyx*), and in helodermatids points to the possibility that such fat storage is coupled with the inability of these lizards to resist desiccation to any marked degree. For only by retreating to burrows or crevices where the humidity is high can they avoid moisture loss when arid conditions prevail on the surface. In other words, such lizards utilize their reserves to tide them over periods when excessive amounts of water would be lost were they to be abroad and active.

EXCRETION AND ELIMINATION

The need for water retention in reptiles, as in birds, insects, and land gastropods, is satisfied by uric acid secretion. Hence they excrete most of their nitrogenous wastes as the relatively insoluble and innocuous acid, as has been recognized for many years.

Durham (1951) has described the gross appearance of the feces produced by a captive Gila monster. He notes that "the feces consisted of solid matter, semisolid matter, and liquid. [1] The solid, doughy mass was nearly cylindrical and measured 22 millimeters long and 15 millimeters in diameter. It was sufficiently solid, even while fresh, to be lifted without distortion with tweezers. This nearly pure white mass formed the bulk of the feces. [2] The semisolid matter was albumen-like in consistency and of a dull greenish color. Although it would stand alone it was too nearly fluid to be picked

up with the tweezers. . . . [3] The liquid part of the feces resembled urine in density and odor." He adds that "A film of tiny yellowish crystals on parts of the whitish mass proved to be entirely uric acid."

Durham reports that under laboratory conditions the frequency of defecation was not wholly dependent upon food intake. Early in the summer the captive defecated approximately once every 2.5 days, but later, with the consumption of eggs remaining at nearly the same level, defecation occurred on the average of only once every four days. "In the dormant, semi-dehydrated condition eliminations were less frequent." Durham provides additional details, the significance of which can be evaluated only when comparative studies of excretion and elimination in reptiles have been carried out.

ECDYSIS

The shedding (molting, exuviation, or sloughing) of the outer layer of the epidermis is commonly observed in *Heloderma*, but precise observations have not been recorded. Shufeldt (1890) observes only that it never "peels off in

great pieces." Garman (1891) reports *H. suspectum* shedding in July; "the epiderm came off in a very ragged way, in shreds and patches." Werner (1913) writes that a *Heloderma* shed in July and November. Englehardt (1914) says

shedding did not occur at intervals but "rather continuously" in a captive. Woodson (1944) claims that ecdysis takes place three to four times each year. Arrington (1930) reports that "the skin is shed at different times of the year, but usually around mid-summer and curls off in small, transparent patches, showing the fresh coat beneath. The region along the vertebrae is the last to shed." Durham (1951) has little to add, but states that in October "great patches loosened first on the abdomen, later on the sides and then on the neck" of an adult. He suggests that molting is a continuous process, although there is no confirmation for this belief. Ten Gila monsters captured the previous summer were examined in the laboratory at the American Museum of Natural History during the months of October and November, and none displayed any evidence that ecdysis was still in progress. All the specimens had molted earlier during the summer. Juveniles may shed more frequently, but it is doubtful whether adults shed more than once during the summer.

The epidermal layer that is shed is translucent rather than transparent as described by Arrington. Evidence of the underlying pattern is readily discernible in the sloughed layer. A brownish deposit is present in it that corresponds to the pattern of melanin in the skin. Hence the pattern of the skin can readily be traced in the exuviae. This, of course, is not unique as far as *Heloderma* is concerned; in most snakes as well as lizards there are deposits of melanin in the cast-off epidermal layer. Rahn (1941) has discussed the problem in snakes, suggesting that melanin is "injected" into the epidermal elements by the branches of the melanophores, as described for birds.

It is not known whether ecdysis occurs more frequently in juvenile *Heloderma* than it does in adults. Fitch (1949) has shown that ecdysis occurs more often in immature than in adult *Crotalus viridis*. Similar changes in the frequency of ecdysis may occur in other snakes and possibly in lizards. However, if exuviation occurs more frequently during the early period of life when growth is more rapid, there is no reason to assume that ecdysis is initiated merely by a "tightening of the skin," as is often assumed. Weltzel (1933) points out that ecdysis is a far more complex phenomenon, probably

accompanied by physiological changes. At least in part it is under hormonal control. Noble and Bradley (1933) found an increase in the duration of the period between molts in the gecko (*Hemidactylus brooki*) following thyroidectomy or hypophysectomy. They did not attribute the increase to any direct hormonal effect. Rather they ascribed the prolongation of the period between molts to a general lowering of metabolic activity. Eggert (1933) reports that thyroid activity in *Lacerta* is reduced when molting begins but is accelerated as ecdysis proceeds and rises still higher before the termination of the process.

Thyroidectomy did not prevent ecdysis in the gecko studied by Noble and Bradley. Ratzersdorfer, Gordon, and Charriper (1949) found that in *Anolis* administration of thiourea inhibited the formation of thyroid, but resulted only in an increase in the duration of the molting reaction without prolonging the interval between moltings. In contrast Eggert (*supra cit.*) found that ecdysis did not occur in lacerids after the thyroid had been removed. The experiments of Noble and Bradley (*supra cit.*) indicate that the pituitary is involved in ecdysis, and Rahn (*supra cit.*) reports that hypophysectomy, or merely the removal of the pars intermedia, does not prevent ecdysis in the rattlesnake, although it results in the complete concentration of melanophores. Evidently, therefore, there are differences between species in the nature and possibly in the extent of the hormonal control of ecdysis.

Bruner (1912) has described what he calls the "swell mechanism" in the heads of lizards, the chief function of which he believes is to aid in exuviation. He observed the operation of the mechanism only in iguanids, and he indicates that it is present in other lizards. According to Bruner the mechanism, in simple form, is also present in snakes, where he assumes that it is "used for molting purposes." It is not known whether this mechanism is present in *Heloderma*, but the mode of ecdysis might conceivably provide clues concerning relationships.

The outer layer of the epidermis of *Varanus niloticus* is reported by Scherer (1903) to be shed in large pieces, apparently in much the same fashion as it is shed in *Heloderma*. In contrast the outer layer of the skin of *Gerrhon-*

otus is shed in one piece (Pritchett, 1903), turned inside out as it is in nearly all snakes. *Heloderma* more closely resembles *Varanus* than it does this particular anguid, although there is evidently variation among anguids. The skin of *Ophisaurus apus* is said by Posselt (1932) to fall off in shreds, whereas according to H. M. Smith (1946) the skin of American *Ophisaurus* is shed almost entire.

In the limbless *Anniella*, a lizard believed to be related to the anguids but placed in a separate family, the outer layer of the epidermis usually loosens first at the neck, and the lizard slips out of it, "leaving it in tightly pleated cylindrical pieces," according to Miller (1944). We have observed ecdysis in the Cuban *Typhlops lumbricalis*, where the epidermal layer is not shed in one piece, as it is in most snakes. Rather the coverings of the individual scales are sloughed off in a series of rings comprised of the coverings of scales from vertical rows of scales that encircle the body, and these rings of scales tend to be telescoped as the snake crawls through the soil. There is no evidence of any interstitial skin between the overlapping scales in the exuviae. The outer layer of each individual scale tends to remain attached to the scales bordering it laterally, probably owing to the presence of the moist excretions from the skin at the time of ecdysis.

Thus the mode of ecdysis in *Typhlops* more closely resembles that of *Anniella* than that of *Gerrhonotus*. In contrast the outer epidermal layer of *Leptotyphlops* appears to be shed in one piece, as in most snakes, with impressions of the imbrications of the scales of the live snake present in the shed skin (Klauber, 1940).

Too few data concerning ecdysis in reptiles are available for sound conclusions to be reached. It is manifest that species differ not only in physiological characteristics as far as ecdysis is concerned, but also in the manner in which the outer epidermal layer is cast off. However, there are no obvious phylogenetic implications, nor is there any evidence to warrant the conclusion that correlations exist between modes of existence. No significance can be attached to the fact that *Heloderma* and *Varanus* shed the outer epidermal layer in similar fashion, as they differ in this respect from most snakes, which presumably descended from the same early platynotid stock. However, some significance can be attached to the fact that differences do exist between leptotyphlopids and typhlopids, more especially in view of the conclusions reached elsewhere (McDowell and Bogert, 1954) that typhlopids have their affinities with the Diploglossa rather than with the Platynota.

TOOTH REPLACEMENT

Variations in the dentition of the two species of *Heloderma* are mentioned above in the taxonomic section of this paper, and a summary of dentitional characters is provided in tables 2 and 3. The modifications of the teeth that provide for the conduction of the venom are discussed in a subsequent section of this paper that deals with the venom apparatus as a whole. Here we are primarily concerned with the mechanism of tooth replacement.

The dentition of a number of species or genera of lizards has been described by various authors. However, few detailed studies of tooth succession in lizards have been carried out. To some extent Camp (1923) employs dentitional characters as well as modes of replacement in his classification of lizard families. In the superfamily Anguioidea, to which he assigned the family Helodermatidae, he notes that tooth re-

placement is alternate. McDowell and Bogert (1954), who transfer the helodermatids to the superfamily Varanoidea, note that alternate tooth replacement also characterizes this group. Earlier Bogert (1943a), who was concerned primarily with tooth replacement in snakes, had reported alternate ankylosis of the teeth of both *Heloderma* and *Varanus*, suggesting that the pattern of alternate succession probably had its origin in an early platynotid ancestor that also gave rise to the snakes. He did not point out, however, that replacement teeth in lizards are vertical in the soft tissue prior to ankylosis, whereas during the period of growth the replacement teeth of snakes are in a horizontal position. Thus the teeth as well as fangs of snakes require forward rotation immediately prior to moving into the vacated socket, whereas during their growth the replacement teeth of

TABLE 2

DENTAL AND SKELETAL CHARACTERS OF *Heloderma horridum*

Source of Information	No. of Teeth					No. of Vertebrae				Total Vertebrae
	Premaxillary	Maxillary	Pterygoid	Palatine	Dentary	Cervical	Dorsal	Sacral	Caudal	
Duméril, Bocourt, and Mocquard, 1878 (1870-1890), 299	6	7-7	—	—	8-8	—	—	—	—	—
Boulenger, 1891a, p. 110	9	—	1-1	2-2	—	—	—	—	—	—
	8	—	6-7	3-3	—	8	26	2	40	76
Taylor, 1940, p. 121	—	—	5-5	1-1	—	—	—	—	—	—
A.M.N.H. No. 57863	9	7-7	4-4?	3-3?	9-9	8	25	2	40	75
A.M.N.H. No. 7216	5	7-6	2-2?	1-2?	9-9	—	—	—	—	—
A.M.N.H. No. 57768	9	7-7	2-3?	3-3?	9?-9?	8	25	2	—	—
M.C.Z. No. 5008	9	7-7	5-8?	2-3	9-9	—	—	—	—	—
M.C.Z. No. 5009	9	7-7	4?-5	3-4	9-9	—	—	—	—	—
M.C.Z. No. 5010	11	7-7	4-6?	4-5	10-10	—	—	—	—	—

lizards advance laterally (or forward on the premaxilla) to the position of ankylosis, without any rotation of the replacement teeth being

required.

Odermatt (1940) reports detailed studies of the teeth in *Heloderma horridum*, although he

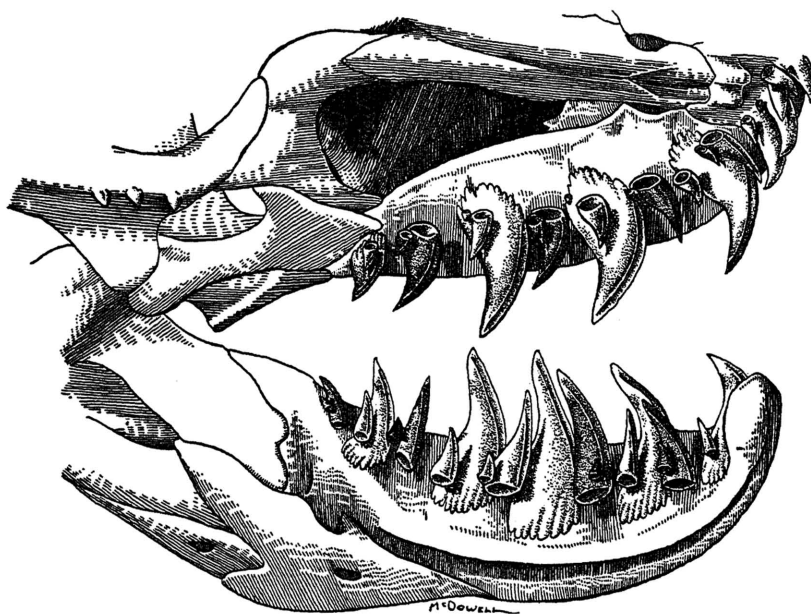


FIG. 31. Lingual views of the upper and lower jaws (left side) of a juvenile *Heloderma suspectum*, showing the relative size and position of the replacement teeth. Drawing by S. B. McDowell, from cleared specimen.

TABLE 3
DENTAL AND SKELETAL CHARACTERS OF *Heloderma suspectum*

Source of Information	No. of Teeth					No. of Vertebrae				Total Vertebrae
	Premaxillary	Maxillary	Pterygoid	Palatine	Dentary	Cervical	Dorsal	Sacral	Caudal	
Shufeldt, 1890, p. 218	—	—	—	—	—	8	27	2	27	64
Cope, 1900, p. 481	8	—	0-0	0-0	—	—	—	—	—	—
	8	—	0-0	2-1 ^a	—	—	—	—	—	—
Boulenger, 1891, p. 110	—	—	—	—	—	8	28	2	27	65
	6	—	0-0	0-0	—	—	—	—	—	—
	—	—	—	—	—	8	26	2	27	63
Taylor, 1940, p. 121	—	—	2-2	0-0	—	—	—	—	—	—
	—	—	2-2	0-0	—	—	—	—	—	—
	—	—	0-2	0-0	—	—	—	—	—	—
S.U.N.H.M. No. 10047	7	8-9	4-3	0-0	9-9	—	—	—	—	—
A.M.N.H. No. 71187 J	9	8-8	4-3	0-0	9-9	8	27	2	28	64
A.M.N.H. No. 66998 ♀	8	8-8	2-2	0-0	9-9	8	28	2	22+	62+
A.M.N.H. No. 71082 ♀	9	8-8	1-0	0-0	9-9	—	—	—	—	—
A.M.N.H. No. 71864 ♂	8	9-8	2-1	0-0	9-9	8	27	2	27	64
A.M.N.H. No. 72908 ♂	8	8-8	3-3	0-0	9-9	8	27	2	24	61
A.M.N.H. No. 72748 ♀	7	8-8	2-3	0-0	9-10	8	28	2	23+	61+
A.M.N.H. No. 72646 ♀	7	9-9	1-2?	0-0	9-9	8	27	2	27	64
A.M.N.H. No. 72999 ♂	8	9-8	1-0	0-0	9-9	—	—	—	—	—
A.M.N.H. No. 73835 ♂	8	8-8	3-3	0-0	9-9	8	27	2	28	65
A.M.N.H. No. 73771 ♂	8	9-8	1-2	0-0	9-9	—	—	—	—	—

^a Cope, probably through a *lapsus calami*, says "... two rudiments on the palatine [intended for pterygoid] on one side and one rudiment on the other." Taylor (1940) reports no palatine teeth on three skulls of *suspectum* that "Cope examined." Though present in *H. horridum*, it is doubtful whether palatine teeth occur in *suspectum*.

devotes more attention to the structure of the functional and replacement teeth than he does to the mode of succession. His figure (p. 114) showing the position of the replacement teeth in the maxilla suggests that such teeth are laid down in rather haphazard fashion in the soft tissue investing the inner side of the jaw. The position of the replacement teeth in Oudematt's material may have resulted from artifacts of preparation or from other causes. Our examination of a cleared specimen (fig. 31) indicates that successional teeth are arranged in the soft tissue in a rather orderly manner.

Bogert (*supra cit.*) has described the mechanism of tooth succession in snakes, pointing out that ordinarily only the alternate teeth in any one series are ankylosed to the bone. Teeth move into position in vacant sockets where they become ankylosed at approximately the same

time that the teeth in alternate sockets are shed. The teeth in any given series are replaced from front to back in two successions, one involving the even-numbered teeth and the other the odd-numbered teeth. Replacements, in progressive stages of growth, are in line posterior to each socket, with those for any two contiguous sockets staggered in size as well as in position. If, for example, the odd-numbered teeth have recently become ankylosed, there may be three teeth in progressively earlier stages of growth behind each socket. However, replacements in line for each even-numbered socket will include one almost fully formed tooth, followed by three partially formed teeth, each of which will be less advanced than its predecessor, and each of which is in an earlier stage of growth than the corresponding rudiment in the series behind the odd-numbered sockets. In other

words, four stages in the growth of each individual tooth are present for each socket, with those for the odd-numbered sockets more advanced than those of the even numbered sockets. This, of course, applies to the situation at one particular stage. As the process of tooth replacement is carried on, the situation for odd- and even-numbered sockets will be reversed. The number of discernible rudimentary teeth in line for any one socket is not constant in snakes, however, some species having more than others.

Somewhat the same sort of tooth replacement mechanism is present in *Heloderma*, but our examination of the teeth in a juvenile specimen of *H. suspectum* cleared and stained, in addition to several skulls, leaves doubt whether the teeth are replaced in regular succession from front to back. In the cleared specimen the right and left sides of both jaws are in the same condition. In the maxillae teeth are firmly ankylosed, counting from front to back, in sockets 2, 4, 6, and 8, with nearly mature teeth partly in place but not ankylosed in sockets 1, 3, 5, and 7. On the inner side of each ankylosed tooth there are two rudiments, one of which is barely discernible, consisting only of the pointed tip. On the inner side of the tooth that is moving into position but not yet ankylosed, only a single rudiment is present. It is intermediate in size between the two rudiments in position to replace the ankylosed tooth (fig. 31).

If we were to judge only by these maxillae, the situation is virtually identical with that encountered in many snakes. However, examination of the teeth in the lower jaw discloses teeth to be firmly ankylosed in sockets 1, 3, 5, 6, and 8, with unankylosed teeth present in sockets 2, 4, 7, and 9. In six additional skulls representing both species, perfect alternate succession is indicated in only about half of the series. That is, only odd-numbered or only even-numbered teeth are ankylosed in the maxilla, dentary, or premaxilla in but 17 bones of the 32 examined. In the other 15 bones the teeth of some contiguous sockets, more often near the middle of the series, were ankylosed.

There is, therefore, reason to doubt whether the teeth in any given series are replaced from front to back in two successions, at least with the precision that they are in the majority of snakes. Alternate explanations are possible:

(1) either the replacement mechanism is in an early stage of its evolution and not yet perfected in *Heloderma*, or (2) a more complex mode of succession exists in lizards of the genus. On the basis of the tabulations of vacant and occupied sockets in the material at hand, it cannot be ascertained whether succession is always from front to back. The presence of ankylosed teeth in contiguous sockets, however, points to the possibility that teeth are replaced from back to front, as well as in the reverse order. In this connection it is of interest to note that Parrington (1936) found evidence of tooth replacement in mosasaurs, "starting at the back of the jaw."

There are other possible explanations. The proportionate size of individual teeth in *Heloderma*, with the larger teeth falling near the middle of the series in both the maxilla and dentary, suggests the possibility that more time is required to replace the larger teeth than the smaller ones at the extremities. Whatever explanation may be correct, it is evident that tooth succession is essentially alternate, even though there is a somewhat greater tendency for ankylosis to occur in contiguous sockets in the larger teeth at the middle of both the maxilla and the dentary.

Examination of the skulls of a few species of *Varanus* indicates that the replacement mechanism in the monitors is essentially the same as that in *Heloderma*. In general there is alternate occupancy of contiguous sockets in the jaw, but occasionally two teeth are ankylosed in adjacent sockets. However, as shown by Bogert (*supra cit.*) there may be five rudimentary replacement teeth in line behind a vacant socket in *Varanus komodoensis*, in contrast to the two of *Heloderma*. Suitable preparations for other species of *Varanus* have not been available, although it seems probable that other species of the genus may conform more closely to *Heloderma* in this respect.

A few skulls of anguids have been examined for comparison. In *Gerrhonotus* sockets were vacant at infrequent intervals, and there is no evidence of alternate succession of teeth. In *G. multicaudatus webbi* two empty sockets often alternate with two in which the teeth are ankylosed. In *Diploglossus millepunctatus* alternate teeth are missing only in the anterior of the jaw, while in *Ophisaurus apus*, where

rounded rather than pointed crowns are present on the teeth of the adult, there are no vacant sockets, although some mechanism of tooth replacement was presumably present in the living animal. It is plain, however, that tooth replacement in *Heloderma* conforms more closely to that of *Varanus* than it does to that of the anguids. Furthermore, the teeth of both *Varanus*

and *Heloderma* are almost fully formed before being moved into position in vacated sockets. In most anguids teeth are in the socket position prior to the formation of the base of the tooth, and there are evident differences between anguids and the varanids or helodermatids in the mode of attachment.

COLOR CHANGES

The literature dealing with color changes in reptiles has recently been reviewed by G. H. Parker (1948). As may be noted from Parker's discussion, numerous investigations have been made of the mechanism of color change in lizards, particularly iguanids, and geckos. However, relatively little attention has been given to lizards in other families, especially those with less spectacular color changes.

Shufeldt (1890), speaking of Gila monsters, reports that "when I have closely watched them they possess to a certain extent chameleonic powers, for I have observed the orange part of their scaly armour pass from that colour to a decided salmon tint and *vice versa*, remaining normally, however, at some shade of orange or yellow." It would be inferred from this statement that a change in hue occurs within a relatively brief period. No other author reports such rapid changes in color, and it seems doubtful whether it occurs.

It has been noted, however, that captive Gila monsters often lose the brilliant salmon pink coloration that commonly characterizes adults at the time of capture. Carefully controlled experiments to ascertain the extent of the change in color or the amount of time that is required have not been made, although it has been recognized that there is extensive variation in the color in many local populations of both species of *Heloderma* under natural conditions. Arrington (1930) who observed the population of *H. s. suspectum* in the vicinity of Tucson, Arizona, comments on the variability, stating that the color varies from creamy white to a reddish orange. "The most common color is salmon, though pale yellow, dull yellow, flesh and pinkish are often found." Arrington does not state whether his observations are confined to adults. However, all the juveniles whether alive or preserved, are characterized by a yellowish rather than a reddish coloration

of the ground color, as nearly as we can ascertain. The reddish coloration appears to be acquired by most individuals later in life. In some instances the yellowish coloration of the juvenile is probably retained for a greater period of time than it is in others, and some individuals never undergo the change from yellow to salmon, especially in the subspecies *H. s. circumscriptum*, where other elements of the juvenile pattern are retained. No one has reported detailed observations encompassing a sufficiently long period of the growth of a juvenile *H. suspectum* to ascertain when the change from yellowish to reddish occurs and our inferences concerning such changes are based largely on observations of the coloration in recently captured specimens of various sizes.

We have observed the change from reddish to yellow in one adult. A Gila monster obtained in Pima County, Arizona, in July, 1950, was photographed in color two days following its capture, at which time it had the salmon pink coloration with a black reticulum characteristic of most adults. When photographed in color over a year later, the ground color had faded to a dingy yellow. It has not been ascertained whether such changes in the pigmentation result from environmental effects or from the changes in diet to which captives are usually subjected. The specimen that underwent the change under laboratory conditions was fed a mixed diet of the eggs of the domestic fowl and pigeon, horse meat, hamsters, and white mice, none of which would have been available in its native habitat.

Stahnke (1950) cites an unpublished manuscript by Maarsingh with the title "The effect of certain environmental stimuli on the coat color of the Gila monster." Through the courtesy of Dr. Herbert L. Stahnke of Arizona State College we have seen an abstract of Maarsingh's paper. As indicated in this ab-

stract Maarsingh sought to ascertain the effects of providing insufficient food, of exposing Gila monsters to ultraviolet light, to white surroundings and constant exposure to light, as well as to dark surroundings, and finally to injections of adrenalin.

Maarsingh states that he kept records of weights and measurements, and made photographs at the beginning as well as at the conclusion of his experiments. An unspecified number of animals were maintained under conditions approximating those existing prior to the initiation of the experiments; these animals served as controls. The duration of the experiments is not indicated in the abstract, although it is mentioned that animals being tested for the effects of starvation were supplied with food on August 19 and again on October 12. Hence it may be inferred that some experiments lasted for a period of months.

It is not evident from the abstract of Maarsingh's study whether he was hoping to induce changes in the hue of the ground color or the changes in the pattern that occur during the ontogeny of *H. s. suspectum*. He indicates that negative results were obtained from his experiments. The ontogenic changes in the pattern of the various subspecies of both *suspectum* and *horridum* are described in the taxonomic section of the present paper, and Cope (1900) commented on them in *suspectum* years ago, noting that "with increasing age the rings become broken up, and the pattern becomes an irregular, coarse reticulation of blackish embracing the yellow tubercles." In view of the fact that such changes occur during the period of early growth during the

course of at least two years, it seems probable that the change results from the effects of one or more of the hormones associated with growth. It is unlikely that such ontogenetic changes would be accelerated by injections of adrenalin or by changes in the environment.

The present state of our knowledge concerning color changes in helodermatids may be summarized as follows: Ontogenetic modifications in pattern that occur during the early years of growth involve changes in the color of individual scales from black or blackish to yellowish or reddish as the banded pattern of the juvenile is replaced by a more complex dark reticulum characteristic of the adult pattern. (A summary of the changes undergone during the ontogeny of individuals of each subspecies of this paper accompanies the description of each, above.) Along with the change in the pattern of *H. s. suspectum* there is a tendency for the yellowish color of the juvenile to darken or become reddish with increasing age. Under some conditions in captivity there is a reversal of this trend in at least some adults, the ground color of which fades from reddish to yellow. It is uncertain whether similar changes occur in the lighter elements of the pattern in *H. horridum*, but after a few years of captivity specimens of *H. h. horridum* rarely have the brilliant coloration usually seen in individuals prior to capture.

There is no confirmation for Shufeldt's (*supra cit.*) statement that Gila monsters possess "chameleonic powers." The adaptive significance of the pattern and color is discussed elsewhere in the present paper.

SENSES

Various authors have commented on the senses or intelligence of the Gila monster. Virtually all their statements are based on evidence of dubious value. Shufeldt (1890) writes that "by a series of simple experiments I have been enabled to satisfy myself that the senses of sight, smell, and hearing are all quite acute in these reptiles, and they are also sensitive to the sense of touch." Shufeldt adds that "as to their general intelligence, however, or such mental attributes as they may be possessed of, I have made no special investigations, but from my

casual observations I am inclined to believe that they stand rather above the average reptiles in both these respects." Cope (1900) says that a specimen "became rather tame, and showed a liking for having the top of its head scratched with a stick. It showed more than usual interest in passing events, raising itself on its fore feet, and elevating its head as though listening."

Arrington (1930) describes what he terms the "natural actions of a typical specimen" when seen in the field. "As we approach, the

animal hears us or possibly feels our tread. It stops instantly, regardless of the position of its body, and listens intently, staring with its beady, obscure eyes in the direction of the disturbance."

Such casual observations, of course, provide little evidence on which to base conclusions concerning the acuity of the individual senses in *Heloderma*. Too few actual experiments have been carried out to permit us to deal with the senses and behavior of these lizards on a scientific basis. The following is little more than an annotated summary of anecdotal accounts, supplemented by descriptions of our own observations.

CHEMORECEPTION

Owing to the difficulty of distinguishing between olfaction and gustation, these senses are commonly discussed collectively as chemoreception (von Frisch, 1926; Warden, Jenkins, and Warner, 1936). Chemoreception may be employed in mating or food-getting activities, as well as in enemy recognition (see also Abel, 1951).

Comparatively few studies of chemoreception in lizards have been carried out. Most of the pertinent literature is reviewed in an earlier section of the present paper where food and feeding habits of the two species of *Heloderma* are discussed. As noted in this discussion, it is virtually certain that all lizards with the protrusible forked tongue employ the tongue-Jacobson's organ mechanism in chemoreception. No thorough investigation has been made, but it is generally believed (von Frisch, *supra cit.*; Hemplemann, 1926) that few if any other chemoreceptors are present in the buccal cavity. Prosser *et alii* (1950) evidently overlooked the papers by Kahmann (1932), Noble and Kumpf (1936), and Payne (1945) when they state (p. 456) that the sense of smell is not well developed in reptiles, although the statement would apply to some species that depend largely on vision.

Underwood (1951) points out that the Ascalabota (including gekkonids, iguanids, agamids, and chameleontids) of Camp (1923) are principally sight feeders and seem to be relatively dependent upon Jacobson's organ in finding their food. In contrast the lizards placed by Camp in the Autarchoglossa, a group that

includes, among others, the scincids, anguids, varanids, and helodermatids, as well as several burrowers, rely more on the sense of smell, with a tendency for olfaction to supersede sight as the important sense in food finding.

Information now available for helodermatids tends to confirm Underwood's assumptions as far as these representatives of the Autarchoglossa are concerned. As discussed in the section on feeding habits, when under conditions in which it is doubtful whether visual cues can be employed, both the Gila monster and the *escorpión* locate eggs that are buried in the sand. It was also observed that a Gila monster displayed some ability to follow the circuitous path left by an egg that had been dragged over the surface of the sand, whereas the lizard failed to see the egg even when it was approached to within 15 cm.

As a further check, a piece of cork approximately the size and shape of a quail's egg was repeatedly placed in front of active, hungry Gila monsters, all of which ignored it. However, when the same piece of cork was rubbed with raw egg yolk, it was promptly seized by a Gila monster that attempted to engulf it. The cork was impaled on its teeth following its efforts to grasp it, whereupon it was rejected. It is evident, therefore, that the Gila monster employs chemoreception in selecting its food, although other cues were presumably employed in the rejection of the artificial egg.

Stahnke (1950) reports that five days after a captive Gila monster had eaten a juvenile rabbit it was offered a four-day old rabbit "on a handkerchief." Apparently the mammal was actually covered by the handkerchief, however, as Stahnke goes on to say that a Gila monster moved to the vicinity of the rabbit and "nuzzled it through its cloth cover." After spending several minutes in an attempt to get directly at its quarry, the lizard finally bit it through the cloth. It is not certain from Stahnke's description whether the rabbit was completely hidden, but after locating a rent in the cloth, the lizard finally pulled the rabbit from it and ate it. Stahnke does not offer any interpretation of these observations, but it is probable that olfactory cues attracted the lizard to the supposedly hidden rabbit and account for the recognition of the mammal as suitable prey.

Durham (1951) believes that vision in *Helo-*

derma is poorly developed but that the sense of smell might be acute. He states that the Gila monster he observed under captive conditions appeared to locate eggs merely by accident or by trial and error. In view of the fact that in our laboratory eggs of the domestic fowl were repeatedly located and devoured when buried in a large cage, it is certain that excavations were not made at random. Furthermore, the presence of the eggs of turtles and lizards in the digestive tract of *H. h. horridum* preserved immediately after capture indicates that such foods are not fortuitously located. The vast majority of such reptiles bury or carefully conceal their eggs. Maier and Schneirla (1935) are doubtless correct in their statement that accident is not a major factor in the finding of prey by reptiles.

Chemoreception probably plays a significant role in the reactions of Gila monsters to other animals. When a large toad (*Bufo alvarius*, a species that inhabits large portions of the range of *H. s. suspectum*) was encountered by a Gila monster engaged in exploratory movements within the laboratory cage, the lizard repeatedly thrust out its tongue as it approached the amphibian. When sufficiently close so that the tips of the tongue nearly came in contact with the toad, the lizard paused after withdrawing its tongue and then slowly backed away before turning to one side to continue its explorations.

Without further experiment it cannot be stated with certainty that chemoreception, principally olfaction through the tongue-Jacobson's organ mechanism, is the dominant sense modality in the behavior of *Heloderma*. Nevertheless, there is reason to believe that olfaction is acute in the lizards of the genus, and probably it is the most important sense employed when hunting food.

VISION

The visual acuity of *Heloderma* has not been scientifically tested. However, several inferences concerning vision within the genus have been drawn from the comparative anatomical studies of Walls (1934a, 1934b, 1940, 1942a), who summarized much of the information available in his well-known book (1942b).

The eye is similar in both species of *Heloderma*. In proportion to the size of the lizards the eye is small. In a relatively small adult

H. s. suspectum, with a head 40 mm. wide at the temporal region, the horizontal slit of the eye when closed is only 7 mm. When the lids are separated the cornea is exposed for a horizontal distance of 5 mm. The lids are rarely parted more than enough to expose the slightly vertically elliptical pupil (in one specimen of five examined alive the pupil was nearly round), which in dim light is approximately 1.7 mm. in vertical diameter. The iris is dark brown so that it can readily be distinguished from the black pupil only under magnification. When shifted from dim light to bright light there is some contraction of the pupillary aperture. As Walls (1942b) notes, there is very little spontaneous mobility of the eyes, a characteristic of "many of the more sluggish, less eye-minded lizards." However, the eyes of *H. suspectum* are not quite "fixed," as Walls states, but movement is decidedly limited as compared with a king snake, for example. Some other lizards, of course, have considerably more mobile eyes.

The eye of *Heloderma* is closed by raising the lower lid, as in most but not all lizards, some of which are able to move both, whereas others lack movable lids. Unlike pygopodids, xantusiids, and the geckos, which are more strictly nocturnal in habits, the Gila monster and its allied species have not evolved a spectacle, nor is there evidence of any tendency towards development of a "window" or transparent plate in the lower lid such as that present in *Lanthanotus*, long referred (erroneously) to the family Helodermatidae. Walls (1934, 1942b) ascribes the evolution of the spectacle to the need for protection of the eye in burrowing or nocturnal reptiles. He believes that the tertiary spectacle has evolved in the lizards of the families Xantusiidae and Gekkonidae owing to their nocturnal, creeping habits, with their eyes "in constant jeopardy from gravel and stubble, amidst which they crawl under such poor visual acuity conditions that they cannot possibly see them clearly enough to avoid them." According to Walls's view, the larger reptiles, including crocodilians and the Gila monster, "are capable of holding the head well above all rigid perforatives," and consequently there has been no selective pressure favoring the evolution of the spectacle over movable lids. This is doubtless an oversimplified explanation of the evolutionary phenomena in-

volved; such factors as the strong tendency for smell to supersede sight as the important sense in the food-finding activities of the *Autarchoglossa* (Underwood, 1951) are possibly involved in the retention of movable eyelids in *Heloderma*. The spectacle appears to have evolved more often in burrowing or secretive, crevice-dwelling lizards, but there are notable exceptions.

The relatively small eyes of *Heloderma* appear to be satisfactorily protected by the thick, scale-covered lids and the whitish, opaque, nictitating membrane, which sweeps the cornea from front to back simultaneously with the closure of the lower lid. The membrana nictitans, evolved as a fold of the conjunctiva at the anterior or inner corner of the eye, is present in most lizards lacking the tertiary spectacle. In *Heloderma* the nictitans, which functions to moisten or lubricate the cornea, is provided with a beveled edge, with an outward-projecting flange. This flange, which appears superficially to be cartilaginous, serves to catch particles of dust swept from the cornea, and to carry them to the forward corner of the eye where they are ejected or deposited. There is no evidence of any mechanism for the protrusion of the eyeball as a means of eliminating sand from the eye as described for *Uma* by Stebbins (1944), who suggests that such a mechanism may be of general occurrence in lizards.

As noted above, the pupil of *Heloderma* is ordinarily vertical elliptical (but subject to some variation), although it cannot be contracted to the slit as it can in geckos and *Xantusia*. Walls (1934), however, describes the pupil of *Heloderma* as being "small and circular," suggesting that there may be some relationship between the retention of eyelids and the supposedly round pupil. He tends to emphasize the nocturnality of helodermatids. As we point out elsewhere, these lizards do not confine their activities to the hours of darkness, which may account for their lack of those specializations seen in species that rarely if ever venture out in the daytime.

Walls is perhaps unnecessarily disturbed by the fact that *Heloderma* has no well-developed rods in the retina. He observes that "The visual cells of *Heloderma* fit the conventional lacertilian plan—single and double elements, all

with oil droplets. The latter are completely colorless and of ordinary size. Rhodopsin is lacking and there is no trace of a fovea [present in pygopodids and most species of *Xantusia*, Walls, 1942b]. The outer segments are more massive than those of diurnal lizards, but do not approach in volume those of some even more rodlike droplet-bearing cells. . . . The visual cells of *Heloderma* have become sensitive enough to make the depigmentation of the oil droplets worth while, but not enough to demand a departure from the [occasionally] circular pupil."

Walls (1934) ascribes the Gila monster's capacity for nocturnality to the extensive summation performed by the bipolar and ganglion cells. "Thus *Heloderma*, a sluggish egg-eater [which it is, in part, but not exclusively, as it also preys on juvenile rodents and lagomorphs as well as lizards], is to be interpreted as a form which has gained the sensitivity needed for scotopic activity largely through summation. There is no need for a truly profound alteration of the visual cells themselves, for the habits of the animal are such that it tolerates the low acuity which was the inevitable result of its choice of method of scotopic adaptation." Later Walls (1942b) mentions that the ciliary muscle, which may be massive in some nocturnal lizards but greatly atrophied in others, is absent in such species as *Xantusia henshawi* and *X. vigilis*, as well as in *Heloderma*, "as if the animal had abandoned all attempts to accommodate."

To summarize the general implications of Walls's findings, there is no evidence that *Heloderma* is highly specialized for nocturnal vision. Rather, the modifications of the structures of the eye appear to be those that might equip *Heloderma* for a partly nocturnal existence. However, contrary to Walls's assumptions, the lack of specialization for nocturnal vision can probably be attributed to the fact that chemoreception, particularly the tongue-Jacobson's organ mechanism, plays a more important role than vision in the food-finding activities of *Heloderma*. Experiments described above under the heading Means of Locating Food point to the utilization of olfactory cues in following trails, locating eggs buried in the sand, and other food-getting activities. As noted there, a Gila monster displayed some ability to trace the

path left by an egg dragged over the substratum, but repeatedly failed to detect the presence of an egg by means of visual cues, even when it came within a short distance of it.

On the other hand, vision may play some part in the behavior of *Heloderma* as shown by the fact that, when stimulated by the scent of food, the same captive was attracted to a moving object outside the glass walls of its cage and tried repeatedly to grasp the object when it was shifted in position. These observations suggest that vision may be of importance in detecting movement, but it is doubtful whether it is of much value to *Heloderma* in locating stationary objects, including its normal food.

There have been few investigations of color vision in reptiles. Wagner (1932) reports evidence of color discrimination in *Lacerta agilis*, but no adequately controlled experiment dealing with lizards has been reported. The partial adaptations for a semi-nocturnal existence in *Heloderma* create some doubt whether color vision is present, but too little is known to warrant speculation.

THERMORECEPTION

Temperature tolerances are discussed in some detail in a subsequent section of this report, where it is noted that Gila monsters are voluntarily active only within the range of 24.2° C. to 33.7° C. (cloacal temperatures). Other lizards are considerably more stenothermic and hence possibly more sensitive to changes in the body temperature. However, it is plain that *Heloderma* avoids extreme temperatures, presumably retreating to the shade provided by rock crevices or rodent burrows whenever environmental conditions on the surface preclude the possibility of regulating the intake or the loss of heat by other behavioral means.

Virtually nothing is known about heat receptors in lizards, but it has been assumed that they are present in the epidermis. Evidence of a temperature-sensitive center in the hypothalamus has been reported by Rodbard (1948), who found that warming this portion of the brain in a turtle caused an immediate rise in arterial blood pressure. However, the thermo-

regulatory mechanism involves not only receptors and the central nervous system, but probably requires a complex integration of the endocrine system. Edwards and Dill (1935) point out that an important factor limiting the survival of reptiles at temperatures near the upper extreme tolerated is the decreased affinity of their hemoglobin for oxygen. In the Gila monster the oxygen tension for 50 per cent saturation of the blood rises from 32 mm. Hg. at 20° C. to 60 mm. Hg. at 37.5° C.

Whether this change in oxygen tension produces the stimulus that results in the lizard's shifting its position to avoid the absorption of heat when the body reaches higher levels remains to be ascertained.¹ However, the behavior of the Gila monster suggests that it is stimulation of epidermal thermoreceptors that results in the avoidance reaction. Simple tests were carried out with Gila monsters inactive and apparently asleep in a cage to which they had become accustomed during a 10-day period. Usually they were lying beneath a rock shelter, sometimes with the head or anterior portion of the body exposed. When an infra-red light was placed directly over an individual, the lizard would eventually open its eyes and shift its position. In 10 trials the lizards moved when cloacal temperatures reached levels between 30.3° C. and 33.2° C. Gila monsters in the same cage, but not involuntarily subjected to heat, were at rest with cloacal temperatures that varied from 27.3° C. to 29.8° C.

It was impossible to obtain temperatures of the Gila monsters prior to exposing them to heat. Hence it cannot be stated whether the extent of the rise in temperature is a factor of importance, nor was it ascertained whether the rate of heat absorption affects the reaction. The heat lamps employed in each instance were suspended at approximately the same level (ca. 30 cm.) above the animal, but some of the lizards were partly or almost completely protected by rocks from direct radiation. Undoubtedly the epidermis of the lizard was at a higher thermal level than the tissues within the cloaca, where

¹ Randall, Stullken, and Hiestand (1944) report accelerated breathing in lizards, presumably including *Heloderma*, when high concentrations of CO₂ were administered; inhibition, with low percentages.

temperature recordings were obtained, as time would be required for heat to be conducted inward. However, the maximum cloacal temperature (33.2°C.) attained before the lizard shifted its position to avoid the source of heat corresponds fairly closely to the maximum temperature (33.7°C.) voluntarily tolerated by active Gila monsters.

PHONORECEPTION

Scientific studies of hearing have been reported for few lizards. Kuroda (1923) tested a lacertid (*Tachydromus tachydromoides*) and concluded that there was evidence of response (opening of the eyes) to air-borne sounds ranging from 4600 to 12,500 vibrations per second. In view of the fact that Kuroda employed a Galton whistle, which does not produce pure tones, the figures were only approximations. Prosser *et alii* (1950) place the upper limit between 8000 and 10,000 vibrations. Berger (1924) reports that loud sounds produced alteration in the rate of respiratory movements in *Lacerta agilis* and *L. vivipara*, which also responded by opening their eyes. However, no evidence of frequency discrimination was found. Adrian, Craik, and Sturdy (1938) found that the upper limit of nerve response varied with the temperature in other reptiles, and they point out that more precise temperature regulation than that possessed by reptiles would appear to be a prerequisite for frequency discrimination.

Casual observations provide little information of value concerning hearing in reptiles. Burden (1927) observed that under natural conditions the giant monitor (*Varanus komodoensis*) appeared to be oblivious to loud sounds but promptly reacted to visual stimuli. However, Procter (1928) states that two *V. komodoensis* in the London Zoological Garden responded to the voice of the keeper, although she notes that these lizards did not "always pay attention to sounds." From her brief statements it cannot be ascertained, however, whether other senses were ruled out.

No conclusive experimental work dealing with phonoreception in *Heloderma* has been carried out. In response to a loud sound produced immediately above the head of a Gila monster that was resting with its eyes closed

and its body partly extended from a crevice between two rocks in a laboratory cage, the lizard opened its eyes and retreated a few centimeters. Care was taken to eliminate visual and tactile clues. There is no reason to doubt that the Gila monster is aware of air-borne sounds, although the range of sensitivity was not ascertained. It is doubtful whether hearing plays a very important role in the behavior of the lizard.

CONTACT RECEPTION

Tactile receptors have not been identified in the skin of *Heloderma*, but no histological study has been made. The Gila monster does not respond to weak tactile stimuli. At least there is no reaction if the body is touched lightly with a camel's hair brush. However, the lizard does respond by flexing the head or the trunk towards the side of the body to which pressure is applied. If moderate pressure is applied to either of the hind feet, the tail is flexed in the direction of the stimulus.

Many animals that tend to seek out crevices presumably do so in response to a thigmotaxis. Such reactions provide protective shelter, and because both species of *Heloderma* seek seclusion in burrows as well as in crevices or beneath rocks, it might be assumed that such behavior reflects a thigmotactic response. In order to test this assumption, four shelters were installed in a cage containing two Gila monsters. All the shelters had rocks at the side, but two were covered with polished marble slabs and two were covered with plate glass. The lizards consistently shunned those where light penetrated, and came to rest in those provided with opaque marble covers. As the shelters were otherwise similar, it may be concluded that the lizards were avoiding light rather than responding to a thigmotaxis.

EQUILIBRIUM RECEPTION

Most animals orient with respect to gravity, and the helodermatids are no exception. As noted elsewhere, Gila monsters were able to right themselves when turned on their backs even at temperatures a few degrees above freezing. Vision may play some role in geotaxis, but Gila monsters right themselves as readily when blindfolded as they do when their vision is not

impaired. Postural reflexes and the responses of the Gila monster that require muscular coordination are presumably dependent upon proprioceptors, which have not been studied in reptiles.

Kauffeld (1943) reports Gila monsters "resting and sleeping turned over on their backs," mentioning that a specimen of *H. horridum* in the Staten Island Zoo "always sleeps with the ventral side turned up and legs spread wide apart." Such behavior would be most abnormal for a reptile. None of the many helodermatids that we have observed behaved in this manner, and it seems probable that Kauffeld's generalization was based on observations of a pathological individual. There is less likelihood that some unnoticed stimulus produced a state of tonic immobility.

As do the majority of vertebrates the Gila monster displays the well-known nystagmus reactions. When the animal is rotated, the eyes tend to remain fixed on an object as long as possible, with the result that the head is shifted in the opposite direction as long as the motion continues. However, as soon as the rotation is stopped, the head is turned as far as possible in the opposite direction. In more active lizards, such as *Crotaphytus collaris* and *Leiocephalus carinatus*, employed for comparison, the head was repeatedly shifted in the direction opposite to that of the rotation and then returned to the forward position, the usual phenomenon of head nystagmus. If rotated slowly enough, the *Crotaphytus* at first reacted by crawling in the direction opposite that of the rotation in an effort to retain a fixed position in relation to adjacent objects. In contrast *Heloderma* merely turned the head, as described above, or sometimes flexed the body.

The eyes exhibited similar reactions, the pupil continuing to shift from side to side in the socket for a second or so after rotation had ceased. As few as three or four rotations produced the eye nystagmus as well as some shifting in the head. In other vertebrates in which the nystagmus has been studied extensively, these nystagmus reactions have been attributed to proprioceptors in the neck muscles; presumably a similar explanation might apply to *Heloderma*.

TONIC IMMOBILITY

Schufeldt (1891c, 1891d) mentions having "hypnotized" a Gila monster in order to secure a photograph. Shufeldt does not explain how this was accomplished, although the photograph reproduced in his paper indicates that a Gila monster was induced to remain in a supine position. Hoagland (1928), who studied tonic immobility in the iguanid genera *Phrynosoma* and *Anolis*, briefly reviews the literature, noting that such immobile states have been spoken of as "death-feigning" or as "animal hypnosis," on the assumption that the plastic tonus accompanying the state bore superficial similarity to that shown in the cataleptic trance of the human hypnotic subject.

Hoagland reports that *Anolis* is readily immobilized by turning it on its back and applying pressure lightly to the thorax. In our experience iguanids are readily immobilized in a similar fashion. Alligators up to 4 feet in length have readily been induced to remain in the supine position for several minutes after stroking the ventral side of the body. However, when Gila monsters were tested it proved to be far more difficult to induce them to remain immobilized when turned on their backs. Repeated efforts were necessary before one would remain in the supine position. At temperatures below 20° C. it became increasingly difficult, and between 6° and 15° C. Gila monsters promptly regained the prone position whenever they were overturned, even when the belly was stroked.

Maier and Schneirla (1935) note that lizards and other animals become immobilized when sufficiently excited by a sudden stimulus or by repeated stimuli. Hoagland (*supra cit.*) suggests that the onset of tonic immobility is "induced by 'shock' to centers of reflex tonus causing promiscuous discharge of these centers with accompanying inhibition of the higher centers," adding that the "reaction of the 'tonic centers' may at the same time lead to discharge of the adrenal glands by way of their spinal connections thus prolonging the state." Whatever the explanation, it is evident that the state is much more readily induced in many other lizards than it is in *Heloderma*, but the individual that Shufeldt "hypnotized" was doubtless in a state of tonic immobility.

ACTIVITIES

Helodermatids have not been studied extensively under field conditions. A few incidental observations have been reported, but more often collectors promptly seize any individual encountered without waiting to find out whether any information of value can be obtained by watching the animal. Occasionally a Gila monster is found near a burrow, into which it may promptly retreat. But usually helodermatids are found in the open, crossing roads or trails, possibly because they are more easily seen in such conditions. On paved roads they are, of course, quite conspicuous, even at night. Whether they habitually seek refuge in the same burrow or whether territories or home ranges are established cannot be ascertained until studies have been carried out with marked individuals.

PERIODS OF ACTIVITY

The Gila monster is never encountered during the colder winter months. Presumably it retires in a burrow, perhaps usurping that of some mammal, but it is possible that the Gila monster sometimes digs its own or modifies one taken over. Ortenburger and Ortenburger (1926) doubt whether they dig their own holes, as in three or four instances Gila monsters "ran with their lumbering gait toward mammal holes located under large boulders." Information is too fragmentary to be certain. It is exceptional to find a Gila monster abroad between the months of November and March, and the activities of those at the northern periphery of the range in Utah may be even more restricted. Probably Gila monsters do most of their foraging during the summer months, particularly during the rainy season. There is great fluctuation in precipitation from year to year in the regions inhabited, but usually June, July, and August are the months of heaviest rainfall in the portions of Arizona where the Gila monster is most abundant. Except during the early spring, the lizard is unlikely to be found in regions suffering from drought.

Jackson (1941), who supplies more detail than most other authors concerning the time of activity of *Heloderma suspectum* in Arizona, states: "The monsters are seen most frequently in the spring, when they are quite active hunt-

ing mates and food. With the hot weather of May and the following summer months they are rarely seen in sunlight. They hide in shaded spots during the heat of day and prowl at night. The casual observer sometimes concludes, because they are seldom seen in summer, that they estivate during the hot dry season. However, a herpetologist can find the reptiles all year, except in late autumn and winter. He knows their hot weather preference for evening and night hours, and that even at best they are hard to see in their native habitat, so he chooses his hunting hours when most people are at supper or in bed. Howard K. Gloyd, Director of the Museum, Chicago Academy of Sciences, was able to collect a few in July, August, and early September. He obtained them in late evening after sundown. Two were captured just after a heavy thunder shower."

It remains somewhat uncertain whether Gila monsters estivate. As Jackson points out, the inference may erroneously have been drawn as the result of the shift in the time of activity, Gila monsters tending to be diurnal during the cooler spring months but nocturnal as the warmer weather approaches. Nevertheless, Gila monsters are very infrequently encountered in regions suffering from prolonged drought, and it seems probable that they avoid the surface under such conditions; whether they remain quiescent or estivate in their burrows under such conditions is a matter for speculation.

Relatively little information is available for *Heloderma horridum*. Sumichrast (1869) observes that it is rarely encountered during the dry season, while Cuesta Terrón (1930), with similar implications, notes that it is more frequently seen during the rainy season. Gadow (1901) states that helodermatids estivate during the "dry and hot season."

Following heavy rains in the Mexican state of Sonora during the summer of 1942, lizards of the race *H. s. exasperatum* were relatively abundant in the foothills near Alamos. Within less than a week over a dozen specimens were brought in by natives from the immediate vicinity of the town (Bogert and Oliver, 1945), although not all of these were preserved. During the month of November, when there is relatively little precipitation along the west

coast of México, only a single specimen of *H. h. horridum* was encountered between Nayarit and Sonora by one of us (Bogert) who traversed the region by automobile in 1939. This *escorpión* was found crossing the road 12 miles north of Rosario in southern Sinaloa on November 21, an overcast day, preceded by rain during the hours of night. Thomas MacDougall has obtained specimens of *H. h. alvarezii* during the months of November, December, and May in Chiapas. On the Pacific slope of the Isthmus of Tehuantepec, within the range of *H. h. horridum*, specimens have been collected during March (Smith and Langebartel, 1949) as well as later in the summer, between June and September (Hartweg and Oliver, 1940), the period when most collecting has been done in the region. It is probable that the *escorpión* may be encountered during almost any month of the year in México in one part of its range or another.

Both species of *Heloderma* are nocturnal as well as diurnal in their activities. Sumichrast (1864a) indicates that *H. horridum* is semi-nocturnal in habits, rarely venturing from its place of concealment except in the early morning or in the evening. Duncan (1884), with information probably drawn from Sumichrast, says that the *escorpión* "moves principally at night." Hobart M. Smith (1935) mentions that a specimen collected near Huajintlán at the border of the state of Guerrero was taken at night. On the other hand all the specimens of *H. h. exasperatum* obtained at Alamos in southern Sonora were captured during the day. Zweifel and Norris (1955) mention one taken at Guirocoba "shortly after sunrise." The *H. h. horridum* mentioned above that was taken in southern Sinaloa was found crossing the road approximately an hour before noon. Depending upon weather conditions, the *escorpión* is probably abroad at all hours, becoming nocturnal when temperatures rise during the day but venturing out when clouds intercept a large percentage of the sunlight.

The Gila monster is similar in habits, probably more often active at night than during the day, although as Van Denburgh and Slevin (1913) point out, it may be active at any hour. Werner (1913) say it appears to be nocturnal, a captive appearing more active towards evening. Roberta D. Ortenburger (1924) and Ortenburger and Ortenburger (1926) report

finding Gila monsters more often at night than during daylight. They mention finding a copulating pair at 8:30 P.M. on July 14, and their field notes on file in the American Museum of Natural History record one taken on August 12, 6 miles north of Tucson, Arizona, at 10:00 A.M. that "was walking slowly on hard gravel." There was a light rain at the time. Kauffeld (1943) found a male and a female together at 9:30 P.M. in the foothills of the Santa Catalina Mountains near Tucson. Gloyd (1937) mentions that all Gila monsters taken during a summer were "collected in the late evening only, in all cases after sundown. Two were obtained just after a heavy shower." Durham (1951) mentions finding a Gila monster at eight o'clock on the morning of May 14 near Hermosillo, Sonora, México, but does not mention the weather conditions. From the same state Allen (1933) reports one "found in the open at night." In our experience these lizards are active during the daylight hours only when it is raining or when the sky is overcast, but it is doubtful whether their movements are quite so restricted as our limited observations would indicate.

On August 29, 1945, an adult Gila monster was taken on the road at 9:10 P.M., when the temperature of the air at ground level was 27.2° C., with the substratum nearly four degrees warmer. The cloacal temperature of the lizard was 28° C. In the regions inhabited by *H. suspectum* there is usually a fairly steady decline in air and substratum temperatures until the sun rises. Under laboratory conditions Gila monsters are found to be voluntarily active (see the section dealing with thermoregulation) at body temperatures as low as 24.2° C. When air temperatures drop much below this level during the hours after midnight in the spring, it is probable that Gila monsters retreat to shelter. Klauber (1945a) supplies information concerning the time of relative activity of a somewhat more nocturnal lizard, *Coleonyx variegatus*, a gecko inhabiting extensive areas in the American Southwest. Klauber's data indicate that these geckos have been taken between the hours of 4:30 P.M. and 3:59 A.M., with a sudden increase in activity around 7:00 P.M., which reaches a peak between 8:30 and 9:00 P.M. and gradually diminishes afterward. As Klauber points out, his data to some extent reflect the activities of collectors, who com-

monly cease their efforts earlier in the evening. However, collectors working in the arid regions of the American Southwest have found it relatively unprofitable to continue searching after midnight.

It is improbable, of course, that Gila monsters have an activity curve that is identical with that of the more nocturnal gecko. Certainly they are more often abroad during the day than *Coleonyx*, but the peak of their activity is probably after sundown. Laboratory observations are in agreement with those made in the field. Kohlhaas (1941) observes that a caged Gila monster was most active at night. During the summer months this was found to be true of several Gila monsters maintained in a large cage at the American Museum. During the winter months, however, they remained hidden under rocks or in other places of seclusion, emerging only sporadically. During the early spring, from March through April, they became increasingly active during the day as well as at night, but as summer approached their activity became largely nocturnal. Because room temperatures were moderately constant during the winter and spring it seems doubtful whether the activities of *H. suspectum* are dependent solely on thermal factors. Studies of photoperiodicity may provide an explanation.

LOCOMOTION

Numerous authors have commented on the sluggish movements of helodermatids. Sumichrast (1864a, 1864b) describes the *escorpión* as being slow and clumsy, and these or similar adjectives have been applied to the Gila monster by numerous authors (Anonymous, 1879; Shufeldt, 1890; Van Denburgh, 1897; Cope, 1900; to cite only some earlier accounts). Van Denburgh and Slevin (1913) observe that Gila monsters "hasten their gait when one approaches them, but were never seen to run." Anonymous (1879) states that these lizards are "no faster than a tortoise." This is almost true, although the Gila monster is not so deliberate in its movements as the desert tortoise (*Gopherus agassizi*) which shares portions of its habitat. Nevertheless, no other quadrupedal lizards in the regions occupied by helodermatids crawl quite so slowly as the Gila monster and the *escorpión*. Unless a place of refuge is within a few feet, they are easily overtaken, even in rough terrain. It is noteworthy that helo-

dermatids can crawl backward almost as efficiently as they can go forward. Where other lizards would turn around, a helodermatid will often retreat tail first. Kohlhaas (1941) has commented on the ability of the Gila monster to move backward.

The pattern of movement of the helodermatid, while slower than that of the majority of lizards, is found in most tetrapods. In fact it is essentially the same as that described for the salamander (*Triturus*) by Schaeffer (1941). The limbs are moved in the following order: (1) right front, (2) left rear, (3) left front, (4) right rear. The body is flexed towards the hind foot being raised from the substratum, with the tail shifted in the same direction. As the movements are repeated, the body is carried forward in sinuous movements not unlike those of such anguids as *Gerrhonotus*, although the locomotion of the latter is faster.

Shufeldt (1890) states that the "head, body, and tail are all kept in contact with the ground" while the Gila monster is crawling, but this is not true of active, healthy animals under natural conditions. Captives may become fat and lethargic and scarcely raise the trunk off the ground. However, when moving about in their natural habitats, at least on level ground, the body as well as the head and tail is carried well above the ground. The late Mary C. Dickerson's field notes now in the files at the American Museum mention that on the road to Tempe in Arizona in 1912 a large Gila monster was seen. "It stood high on its legs and walked fast. Succeeded in getting into a hole before we could capture him." The *escorpión*, with a proportionately longer tail, may drag the end of the appendage. An emaciated specimen observed in the laboratory invariably did so, but an animal in prime condition may well be able to carry the tail sufficiently elevated to clear the ground. Sumichrast (1864a, 1864b), may be correct, however, in his statement that "very old" examples of *H. horridum*, or females distended with eggs in the oviducts, drag the belly along the ground.

SPEED ATTAINED

The speed attained by a helodermatid doubtless is affected to some extent by the size of the animal, the nature of the stimulus, and to some extent by the temperature, with fatigue and

other factors undoubtedly being involved. Tests were made with a freshly captured individual in Arizona, which was allowed to crawl on a flat, sandy surface. The individual employed was an adult weighing 515.8 grams, with an over-all length of 446 mm., of which 130 mm. comprised the tail. Because Gila monsters tend to avoid direct sunlight, ordinarily crawling as rapidly as possible towards any stationary object on the horizon (a procedure that would ordinarily lead them to a source of shade), the tests were carried out on a clear, warm day, August 16. The starting point was marked in the sand and the lizard was allowed to crawl until it stopped, at which juncture the time was noted and place where movement had ceased was marked. The distance covered was then measured; usually it was sufficiently close to a straight line to avoid difficulties in following the exact trail.

The test was repeated 10 times, during which period the cloacal temperature rose from 22.8° C. to 26.7° C. Distances covered ranged from 7.36 to 10.6 meters. The maximum speed attained during any single test was 21.2 meters per minute, or a rate of 1.27 kilometers (0.79 miles) per hour. The average speed for the several trials was only slightly less, 1.07 kilometers per hour.

DIGGING

Reptile eggs found in the digestive tracts of both species of *Heloderma* indicate that digging is important in their food-getting activities. Sumichrast (1864a, 1864b) reported that it was not unusual to meet *H. horridum* roaming about near holes dug in the sand from which the eggs of iguanas had presumably been removed. An *escorpión* from the Tehuantepec region, where Sumichrast made his observations, did indeed contain a number of lizard eggs, which tend to confirm his belief, although the identity of eggs found in the digestive tract remains uncertain. Lumholtz (1902) mentions that while en route to Santa Teresa in the present state of Nayarit, México, he "killed a Gila monster that was just making its burrow." The specimen mentioned is in the American Museum and is, of course, *H. horridum*. It is problematical, however, whether the lizard was actually making a burrow or digging in search of food. Sumichrast states that the burrows in-

habited are "dug at the roots of trees or under a mass of vegetable debris," but, whether this is based on observation or inference, it remains to be verified.

Gila monsters provided with suitable terrain devote much of their activity to digging. Ortenburger and Ortenburger (1926) observe that "these lizards are powerful diggers. Several individuals which we kept in captivity for many weeks spent entire nights digging with slow persistence in the gravel which formed the bottom of their cage. Several times when individuals were turned loose for the purpose of taking pictures, they immediately turned toward boulders in the vicinity and attempted to burrow under them, digging in the same slow but powerful strokes that were used when digging in their cages."

Garman (1891) observed a captive Gila monster that was kept in a box with several inches of sand and several rocks; "under the side of one of the latter the burrow was made. The digging was all done with the hands; beginning with the left the sand was thrown back with some force in slow strokes, about thirty to the minute, then the right was used in the same way. The motions were outward or lateral, not vertical like those of a dog. For a while the sand was dug out directly, until it began to pour back; then a position was taken up on the top of the heap that had been made, and it was thrown still farther back; gradually working forward, conditions were soon made favorable for continuance of excavation at the bottom of the burrow. At the depth of about a foot the body was hidden and only the tail exposed. This depth appeared to be satisfactory for a time, and the dwelling was occupied as if complete."

Garman also noted that "when the tail was sticking out of the excavation, as in digging, the slender extremity moved from side to side, back and forth and around, with more flexibility than was to be expected from its size, as if constantly on the alert for unseen dangers."

As Garman reported, all digging is done with the front limbs, with the soil carried to the sides of the body. The chin is pressed to the ground, serving as an anchor while the limbs brush the soil backward with considerable force. The movements of the fore limbs during such excavating activities are carried out sys-

tematically, six strokes with the right foot being alternated with five or six of the left, for example. There is some variation, possibly depending on what the lizard encounters as it digs. On March 21, 1951, an adult female was observed excavating a hole in the sand provided in a laboratory cage. Alternate limbs were employed for the following numbers of strokes: left 6, right 7, continuing 9-8, 7-5, 5-6, 4-5, 4-4, 5-7, 8-7, 6-6, 3-9. Digging is interrupted at sporadic intervals while the lizard seemingly pauses to rest. When counts were recorded in this instance there was a total of 129 strokes before the lizard interrupted its activity to remain motionless for approximately four minutes. Afterward it resumed digging briefly before crawling to another part of the cage.

CLIMBING

Over half a century ago Van Denburgh (1897a) reported that "in spite of its clumsy form" the Gila monster "sometimes climbs bushes, probably in search of bird's eggs." In contrast, Sumichrast (*supra cit.*) says of the *escorpión* that "its thick toes could not enable it to climb trees." In an effort to see whether either species could be induced to climb, a small tree with a straight trunk approximately a meter high was installed in a large cage containing three Gila monsters and one *escorpión*. Branches extended laterally at intervals of a few centimeters, the lowermost within approximately 10 cm. of the ground. Not once did we observe a Gila monster attempt to scale the tree, although the *H. horridum* repeatedly climbed to the uppermost branches and descended again, displaying considerable agility in doing so. Thus Van Denburgh's observation would remain unconfirmed did we not have the field notes made by the late Mary C. Dickerson in 1912. Near Tucson she observed two Gila monsters climbing "quite high" in cholla cactus plants. Presumably these were separate observations; her notes are not explicit on this score. Cope (1900) observes that the Gila monster, in climbing up steep places, "utilizes its robust tail as a support, and a very slight hold with the powerful claws of the forefeet is sufficient to enable it to raise itself." Willey (1906) drew a somewhat exaggerated inference, probably from Cope, asserting that the Gila monster

"can raise itself to a considerable height balancing itself on the tip of the tail."

SWIMMING

Every reptile we have ever tested has demonstrated the ability to propel itself while in the water. Even such desert-dwelling snakes as the sidewinder (*Crotalus cerastes*), with its specialized locomotion, can swim. When in the water, however, this small rattlesnake abandons the sidwinding characteristic of its progression on land and resorts to lateral undulatory movements not unlike those of other snakes. It was not astonishing, therefore, to find the Gila monster capable of swimming (pl. 19, fig. 2). Sporadic floods in canyons or washes characterize the region it inhabits, and there can be little doubt that this ability occasionally enables a Gila monster to avoid drowning.

A Gila monster liberated near Cave Creek in the foothills of the Chiricahua Mountains of Arizona at a time when the stream contained water to a depth of 20 to 30 cm. did not hesitate when it approached the bank. It waded into the shallow water along the gradually descending bank, and when the water became sufficiently deep it propelled itself by flexing the body and tail, with the limbs moving occasionally but contributing little to its propulsion. No great speed was attained, however, and the lizard was somewhat more clumsy in the water than it was on land. The *escorpión* is probably equally well prepared to negotiate a stream, but we are unaware of any reports of its swimming. Sumichrast (1864b) believed that "its round and heavy tail could not in any way serve it as an instrument of natation," but he might have been astonished had he placed one of these lizards in water. The tail is manifestly not specially adapted for swimming, but in the Gila monster it does aid in propulsion, and the *escorpión*, with its longer tail, might swim with greater ease.

Aside from their inefficient swimming, which would nevertheless enable them to reach the safety of land in all but the swiftest flash floods that occur in deserts, Gila monsters are not readily drowned. Werner (1913) mentions an individual that was submerged in a pan of water, by implication forcefully, that not only came to the surface but did so in a very "angry" fashion.

FIGHTING

It is questionable whether helodermatids ever engage in combat with others of their own species under natural conditions. Ortenburger and Ortenburger (1926) observe that Gila monsters "were relatively good natured among themselves, and with other animals in the same cage. In no case did they bite the other animals (*Uta* [a small iguanid lizard] or *Scaphiopus* [a pelobatid frog]) which were kept in with them and which would climb over the heads of the Gilas a great many times a day. They did occasionally bite each other, but only in a half-hearted fashion, usually merely snapping a leg of the offending individual and then releasing the hold after a few minutes. When teased they become aggressive and vicious, hissing and blowing and snapping suddenly." Similarly, Werner (1913) notes that "caged companions were unmolested."

Gila monsters kept in the laboratory at the American Museum did not ordinarily molest others of their own species. However, on one occasion a lizard that had been eating the contents of a hen's egg had completed the task, with some of the albumin still adhering to the sides of its head from the edges of the broken shell. Another Gila monster was evidently attracted by the odor of the albumin. It approached, thrusting out its tongue as it did so, and finally lapped the albumin on the lizard's head for a few seconds before it opened its mouth and prepared to bite. As soon as the teeth came in contact with the other lizard's head, the latter withdrew and was no longer molested.

Other animals in the same cage, mostly smaller iguanids, *Sceloporus*, *Leiocephalus*, *Dipsosaurus*, and *Crotaphytus*, and toads, including various species of *Bufo*, were generally ignored at first, even when they came to rest on the bodies of the Gila monsters. This was during the fall and winter. Later, in the spring, when the Gila monsters became increasingly active, principally at night, collared lizards (*Crotaphytus collaris*) which are diurnal in their activities began to disappear. Sources of radiant heat provided in the cages were turned off at night, at which time the collared lizards sought seclusion beneath rocks provided. While the Gila monsters were not seen capturing the smaller lizards, it was evident from the position

of the rocks and the sand in the morning that the Gila monsters had dug the diurnal iguanids from beneath the rocks. Under such conditions, with the collared lizards in a lethargic state as the result of the absence of any source of heat, they must easily have been overcome and devoured by the larger species. Three collared lizards disappeared from the locked cage on as many nights, and there was no doubt concerning their fate, even though it had not been witnessed.

Arrington (1930) asserts that when captive Gila monsters "are vigorously disturbed, an interesting fight will occur. The two belligerent individuals will poise with wide open jaws, in an attitude of two dogs baring their teeth, waiting for an opportunity to strike. Almost invariably the luckless one is gripped by the lower jaw of its wide open mouth with a painful sound of crunching teeth and crackling bones. The aggressor merely hangs on, never relaxing his grip, and permits himself to be dragged in any direction as the less fortunate combatant writhes and rolls in apparent pain. Sometimes the loose skin of the neck is the seat of the attack, and the animals may roll on the ground for as long as ten minutes, their flexible bodies getting into every position. The writer has never seen two of the reptiles battle until death, for there is usually one successful strike made, and whichever animal places his powerful jaws first is conceded the victor. As soon as he sees fit to release his captive, both are content to amble away in opposite directions to rest."

By "vigorously disturbed" Arrington perhaps implies that one lizard was thrust at another, both previously having been stimulated to the point where they had assumed their aggressive defensive behavior. Under such conditions Gila monsters may well be induced to fight. While many captives become lethargic, even sufficiently so that they may be picked up without resisting, others will continue to emit a loud hiss whenever disturbed. If seized they flex the body and employ the claws as they attempt to free themselves or engage their teeth. As Ruthven (1907) reported, Gila monsters react violently when first captured. If seized with long forceps a Gila monster struggles "fiercely, snapping and hissing and throwing its head from side to side with surprising

swiftness." When the teeth of a Gila monster came in contact with the side of the bag into which Ruthven and his assistant were trying to put it, "it held on with bulldog tenacity, making it necessary to pry open the jaws to free the bag." A Gila monster that one of us captured near Tucson seized the arm rest on the car door as we were obtaining a reading from the thermometer that had been thrust in the lizard's cloaca. The Gila monster retained its grip on the arm rest for slightly more than 15 minutes, with its teeth embedded in the fabric and the layer of "foam" rubber beneath it.

RESTING, SLEEPING, AND BASKING

Helodermatids are usually crawling when encountered in their native state. They may escape notice when at rest, or, as seems more likely, they seek seclusion and remain hidden when inactive. In captivity they spend long periods of time completely immobilized, with the eyes closed and the body relaxed, the limbs outstretched, and the chin, trunk, and tail resting on the ground. They often prefer to draw the body beneath a rock, if this is provided, or they may come to rest in a shallow pan of water.

If they bask under natural conditions, as they probably do, it is doubtful whether they venture far from their burrow, perhaps basking with the body only partly exposed at the entrance. When heat lamps are provided for caged individuals, they often expose only the anterior portions of the body when conditions permit. Shufeldt (1890) notes that when sunning themselves, "they have a habit of stretching their limbs backwards, even to the extent of having the feet with their dorsal aspects in contact with the ground, the palm and soles directed upwards. They will close their eyes and lay [*sic*] in this position for hours at a time." Garman (1891) makes a similar statement: "In sleep the body lies flat on the sand and the arms are usually stretched back, palms upward." However, both species more often rest with the body lowered to the ground, and with the feet in normal position, palms and soles directed downward.

EATING AND DRINKING

The methods employed in locating and devouring small mammals, fledgling birds, raw

meat, carrion, and eggs are discussed in the section dealing with food and feeding habits. However, the manner of ingesting liquids was not described. Garman (1891) describes the action of the tongue of the Gila monster while drinking water or devouring the contents of an egg. Commenting that the five days required to ship the lizard from Arizona to Cambridge, Massachusetts, would not have been a "very long time between drinks" for a desert animal, Garman was evidently astonished that "more than an hour elapsed from the time the snout was brought down to the liquid and the tongue thrust into it until the head was raised and, licking the lips and yawning to disclose the inky blackness inside the mouth, preparations were begun on a sleeping place."

When Garman offered the reptile an egg broken into a dish, it was taken in the same manner as the water. "The chin was dipped into it and the tongue thrust out, bent downward and drawn back again. The tongue is thick and riband-shaped [*sic*], i.e., long, narrow and somewhat depressed. In protrusion it first makes its appearance as a single sharp point; as it comes farther out the tip separates as two points, and the organ is seen to be forked for a short distance. When fully protruded, the aspect is changed and the outline of the extremity, as seen from above, resembles that of the tail of a shad. [And any good Bostonian knows what that is.] As the tongue is drawn in, the tips approach each other till once more closely applied. Thus, the forked portion moves sidewise like the blades of a pair of scissors as the tongue goes out and back. Any of the fluid that adhered was carried into the mouth by the retraction, and no doubt the tongue was followed by a slight current induced by suction that took in a little more; the amount of suction, however, must have been very slight, judging from the time occupied in eating a single egg." It may be added, however, that eggs the size of a hen's are not often encountered under natural conditions, where the smaller eggs of most reptiles or of ground-nesting birds are often engulfed whole, without breaking the shell, whether it be leathery or calcareous.

Garman does not mention that, while the liquid is being drawn into the mouth with the tongue, the head is raised at intervals as though

to pour the contents of the mouth backward into the throat. Van Denburgh (1922), Arrington (1930), and Woodbury (1931) depict the Gila monster in the posture assumed on such occasions. Arrington observes that "in drinking it must elevate its head in a manner similar to that of a chicken," and that "the head is held as high as possible and held in this posi-

tion for some time, while the material runs down the throat to the stomach. A hungry individual will eat three or four ordinary hen's eggs without stopping. Should the reptile be picked up by the tail and held head downward, any time within an hour after eating or drinking, regurgitation follows, so little is the muscular control of the throat."

LIFE HISTORY

REPRODUCTION

THERE IS SCARCELY any precise information concerning the breeding habits of either species of *Heloderma*. The information in print is inadequate for an understanding of the life cycle, and the few data obtainable hardly warrant separate treatment for the two species. What is known may be summarized as follows:

TIME OF MATING

No courtship behavior has been reported for either species of *Heloderma*, and seemingly only *suspectum* has been seen in pairs under natural conditions. Arrington (1930) states that during the first week in March a male and female of *H. s. suspectum* were found together at the edge of a hole that "evidently had been their home during winter hibernation." He says that these were "surely naturally mated," though he does not say how he ascertained the sex, and the female laid no eggs in captivity. Roberta D. Ortenburger (1924) and Ortenburger and Ortenburger (1926) report that "a copulating pair was seen just after dark [Ortenburger's field notes state 8:30 P.M.] July 14, about a mile and a half up one of the canyons [in the vicinity of Tucson, Arizona], and they were out in a hard shower." Between July 8 and July 21, Kauffeld (1943) discovered "a male and female together at 9:30 P.M. in a clump of vegetation in the dry, rocky stream bed of Bear Canyon, northeast of Tucson at 3100 feet altitude." These specimens were later presented to the American Museum, and the sex has been verified by dissection.

From these few reports it seems probable but is unproved that in southern Arizona *H. s. suspectum* mates during July rather than in March. If mating activities are nocturnal, as suggested by the finding of a male and female together after dark, the paucity of observations reported is readily understandable.

In view of the lack of any conspicuous differences between males and females, it seems probable that sex recognition is accomplished by means of behavioral or olfactory cues rather than by means of vision, which plays a more significant role in the activities of the Ascala-

bota than in the *Autarchoglossa* (see Underwood, 1951).

OVIPOSITION

The most complete accounts of egg deposition are those of Ditmars (1907, repeated in 1936) and of Arrington (1930). Cuesta Terrón (1930) ostensibly describes oviposition in *horridum*, but it is apparent that his statements are largely derived from Ditmars' account of *suspectum*. Ditmars in turn obtained his information from a correspondent, Walter Ralston, who had made his observations in "Arizona." It is not plain whether Arrington's account is based on that of Ditmars, on personal observations, or on both. Van Denburgh (1922) and Hegner (1935) evidently obtained their information from Ditmars, who states that a captive laid five eggs (one of which is figured). Ditmars adds that, according to Ralston, the number of eggs deposited by *suspectum* in Arizona varies from six to 13.

In an earlier (1904) account Ditmars says three to five eggs are laid. In 1910 he mentions that a specimen 19.5 inches [495 mm. over-all] long in the New York Zoological Park laid four eggs. Van Denburgh, using Ditmars' (1907) data, reports five to 13, but Arrington says "six to ten eggs," as does Woodson (1944) who probably obtained his data from Arrington. Bendire (1887), recalling a specimen captured near Tucson, Arizona, 15 years previous to his writing, says that if he "remembers rightly" it contained eight eggs. Werner (1913) says that according to "Captain Spring" the number varies from three to four, but the dimensions given for the eggs leave not a little doubt concerning the reliability of the report.

Dissections provide better evidence. Stewart (1891) states that a small specimen of *H. suspectum* contained nearly ripe ova, two on the left ovary, three in the right, and that the largest ovum measured 24 mm. by 21 mm. In southern Arizona Hensley (1950) obtained a specimen of *suspectum* in May that survived until the following October when it was preserved. Examination "revealed five large,

spherical, well-developed but unfertilized eggs in the ovary." These eggs had an average diameter of 36 mm., larger than those in the oviducts of a specimen of *H. s. cinctum* (No. 1932 in the collection of the University of Utah) from near Hurricane, Utah. Our examination of this individual discloses five eggs, four in the left oviduct, one in the right. This specimen, which has a snout-to-vent length of 315 mm., was collected on June 10 and preserved on December 16 of the same year. The eggs, distorted somewhat as preserved in the oviducts, average approximately 24 mm. in diameter, considerably smaller than those Hensley supposedly found in "the ovary." It is not clear from Hensley's account whether he examined more than one ovary, although he informs us that both were examined. It is manifest that both are ordinarily functional in adults. The large eggs, however, were probably in the oviducts rather than in the ovary.

A fully grown female of *H. s. suspectum* taken near Quijotoa, Pima County, Arizona, by Mr. George M. Bradt on July 15, 1950, was extremely thin when first obtained; it consumed large quantities of food the following spring and summer while in captivity in the laboratory in New York City, but as far as known no eggs were deposited (see comments by Shaw below). It was kept in a large cage (3 m. by 1.2 m.) with two males, but no courtship or copulation was ever observed. It ate sparingly during the early spring of 1952, and it was found dead on June 3 of that year. Dissection disclosed three eggs in the right oviduct, four in the left. Each of the nearly spherical eggs approximated 25 mm. in diameter prior to preservation. Whether they had been fertilized could not be ascertained. Despite the fact that the specimen had thrived the previous year, conditions in the cage were evidently inadequate for oviposition. Arrington (1930) comments that "occasionally a female will mysteriously die just before its eggs were to have been laid."

During the summer of 1952 four *H. s. suspectum* from the vicinity of Tucson, Arizona, were obtained from Dr. Charles H. Lowe. The specimens had been obtained earlier the same year and had been maintained in the laboratory at the University of Arizona. While in a small cage carried in a motor vehicle one of these lizards laid four eggs on July 29. The

eggs, figured in plate 19, appeared to be normal when discovered the evening after they had been laid. Fifteen days later, after the four lizards had been installed in a large cage in the laboratory in New York City, one additional egg, probably deposited by the same individual although this is uncertain, was found in the cage. This one was considerably smaller.

These reports and meager data thus indicate that the number of eggs in a clutch varies from three to 13, but the upper limit is subject to doubt in view of the fact that more than one female may have used the same site for oviposition. Communal egg laying has been reported for other lizards, and the observations reported by Ditmars do not rule out this possibility in *Heloderma*. Four to seven eggs would seem to approximate the usual number of eggs laid by *suspectum*.

In addition to the five large eggs mentioned by Hensley (*supra cit.*), 25 smaller eggs were removed from the ovaries, and he found that the 30 eggs comprising the total could be sorted into eight groups that varied in number from two, for the smallest eggs, to five for the largest, with five of the groups composed of four. If his assumptions are correct, the maximum number this individual might have produced at one time would, presumably, have been only five.

Ditmars' informant says that the eggs are deposited during July or August, whereas Arrington says oviposition occurs during the month of July, usually the latter part. Werner, on questionable authority as noted above, says the eggs were laid in August. Under the abnormal conditions described above, eggs were laid on July 29, while one, possibly part of the same clutch, was not deposited until August 15. Evidence obtained from captives is not to be considered reliable, but there appears to be some agreement that oviposition occurs within the latter part of July or during the first half of August, and it is probable that even under natural conditions variations result from differences in the temperature or rainfall from year to year.

Earlier oviposition, probably abnormal, has been observed by Mr. Charles E. Shaw. He informs us that a captive *suspectum* in the San Diego Zoological Garden deposited a single egg on June 19, 1950. The egg was doubtfully

fertile, and the time of deposition may have been abnormal owing to the conditions of captivity. Later, in 1952, Mr. Shaw wrote that early in April a misshapen egg was discovered in a cage inhabited by several individuals of *suspectum*, and later two leathery shells found in the same cage apparently had passed through the digestive tract of a Gila monster. Mr. Shaw believes that the eggs laid were devoured soon after deposition by other individuals or possibly by the female that deposited them. Woodson (1949b) quotes an unidentified informant who suggested that *Heloderma* "is not loathe to partake of eggs that it, itself, deposits." This observation may account for the seeming rarity of oviposition by captive individuals.

Large specimens of *H. horridum* evidently deposit more eggs than the average for *suspectum*, and it is probable that the size of the female has some bearing on the size of the individual clutch in both species. The only information thus far obtained is from captives. In *H. horridum* oviposition seemingly occurs during the late fall or winter, following the wet season in western México. Curtis (1949) had a specimen 685.8 mm. in total length from an unknown source in México that deposited 15 eggs at irregular intervals between January 31 and February 20. The deposition of the eggs over a prolonged period presumably can be ascribed to the unnatural conditions of captivity. As Curtis notes, the 21-day period over which the eggs were laid is probably to be construed as evidence of retention beyond the normal date of deposition.

A specimen of *H. h. horridum* 618 mm. in over-all length that was sent to the Instituto de Biología by Señor Iván Pedrero from Placeres de Oro in the lowlands of the Balsas River drainage in Guerrero laid 10 eggs on November 20, 1949. It is probable that this date, which coincides with the close of the rainy season in Guerrero, is more nearly normal. In the absence of better data, it is presumed that oviposition normally takes place prior to the dry season. *Heloderma horridum* is certainly less commonly active during other months of the year and may indeed be estivating, as has often been stated, largely upon the authority of Sumichrast (1864a, *et seq.*)

Señor Miguel Alvarez del Toro, who provided many of the specimens on which we base

our description of *H. h. alvarezi*, informs us that a female of this subspecies, still living after eight years in the zoological garden in Tuxtla Gutiérrez, Chiapas, deposits four or five eggs each year. Unfortunately he does not state the time of year when the eggs appear, although he has supplied a photograph (pl. 4, fig. 1) that depicts the female and one egg.

In view of the fact that *H. h. alvarezi* appears to be the smallest of the three races of *horridum*, it may deposit fewer eggs on the average than the larger races. Sumichrast (1864a, 1864b), whose papers contain many unverifiable statements, says that "in very old individuals, or in the females before oviposition, the belly acquires a great lateral development, and drags upon the ground." It is conceivable that a gravid female containing a great number of mature eggs might find it difficult to raise the body from the ground while crawling, although the weight of individual specimens is as much dependent upon deposits of adipose tissue as upon age or the gravid condition.

Our examination of the viscera of preserved specimens disclosed no females of *horridum* that were gravid. Such evidence is not entirely reliable, however, as a female containing a large number of eggs would be difficult to preserve, and such specimens may either have been eviscerated or have become decomposed or destroyed so that they were not represented in the sample. It is equally possible that gravid females are less frequently encountered, perhaps because of more secretive habits after ovulation has taken place.

Ditmars (1907, 1936), mentions that "several specimens [of *H. suspectum*] captured by Ralston [in Arizona] deposited eggs," although no dimensions of the eggs are given. Earlier in his account Ditmars mentions a specimen that produced five eggs. One egg from this clutch is illustrated actual size, indicating that it measured 72 by 35 mm. Arrington (1930) says only that "the egg is quite large, approximating that of a small hen's egg, and has a white, oval, rough shelled covering that is thin though not fragile." Werner (1913) supplies dimensions of 19 by 13 mm., manifestly inaccurate.

Ditmars (1904) and Berridge (1926), who probably copied the original statement, give dimensions of $2\frac{3}{4}$ by $1\frac{1}{2}$ inches, but no one has otherwise recorded the dimensions of the

eggs of *H. suspectum*. There may be some doubt whether eggs deposited by captives are normal in size or shape. However, the dimensions of the first four eggs laid by the specimen obtained from Dr. C. H. Lowe in 1952 were, respectively, 75 by 35, 70 by 33, 72 by 37, and 67 by 39 mm., indicating some variation in size and shape but comparing favorably with the dimensions of the egg figured by Ditmars. Other eggs laid by captives are misshapen or so much smaller as to be considered abnormal.

The only published report that supplies dimensions for the eggs of *H. horridum* is that of Curtis (*supra cit.*), who gives measurements of 12 eggs, which varied from 55 to 60 mm. in length and from 23 to 27 mm. in diameter, the average being 59.6 by 25 mm. The 10 eggs laid by an adult from Guerrero mentioned above averaged 59 by 38 mm., thus having a somewhat greater diameter than those described by Curtis. It is uncertain whether the eggs in either clutch were normal. Pending the acquisition of additional information it must also remain uncertain whether the eggs of *horridum* are actually smaller than those of *suspectum*, as the measurements now available indicate.

REPRODUCTIVE CYCLE

Hensley (*supra cit.*) suggests that the reproductive cycle in *H. s. suspectum* may require two years, basing his suggestion on inferences derived from an examination of a specimen collected in May that contained five large "ovarian eggs" (probably in oviducts) when examined after death the following October. The data derived from our examination of the female that was gravid after more than a year, during which no eggs had been laid, and our examination of the female from Utah mentioned above tend to verify Hensley's assumption. The individual from Utah was taken in June and contained well-developed eggs in the oviducts when it was preserved in December of the same year. Further investigation is necessary, however, before any definite statement can be made.

The information supplied by Señor Alvarez del Toro indicates that the southernmost race of *horridum* deposits eggs annually, but whether this is true of other races also remains to be ascertained. Rahn (1942) has shown that there is a two-year reproductive cycle in the prairie rattlesnake (*Crotalus v.*

viridis) near the northern limit of its range in Wyoming, whereas it is virtually certain that only one year is required to complete the cycle in other parts of the range of the species where rattlesnakes can remain active for longer periods of the year. Similarly Volsøe (1944) has shown that the European viper (*Vipera berus*) may require one or two years to complete its reproductive cycle, depending upon altitude as well as latitude, and hence, indirectly, upon thermal factors. Although a two-year cycle of reproduction has not been reported for any lizard, it is not beyond the realm of possibility that it may occur in *suspectum*, while *horridum*, with a longer season of activity, may require but one year for the completion of the reproductive cycle.

INCUBATION

Virtually all the information in print concerning the incubation of the eggs of *Heloderma* seems to stem from the statements of Mr. Walter Ralston that Ditmars summarized in 1907 and repeated in 1936. The accounts of Van Denburgh (1922) and Arrington (1930) for *suspectum*, despite minor discrepancies in the latter, do not appear to have been based on personal observations, and they cannot be construed as providing verification of the original account. Although Cuesta Terrón (1930, 1934) ostensibly supplies information for *horridum*, it is evident that his account was based largely on what Ditmars reported for *suspectum*, more especially as "Ralston" is quoted in the final sentence of Cuesta Terrón's paragraph dealing with the eggs.

Ditmars states that "the female scoops out a hole in damp sand and deposits her eggs therein, when the sand is shoveled back again, entirely covering the eggs. Several nests were said to have been discovered . . ." and "the majority of the eggs were buried to a depth of five inches." Ditmars says further that "the situation generally selected was open and exposed to the sun for the greater part of the day, though the nest was usually dug near a stream, where the infiltration kept the sand continually moistened." It is evident that Gila monsters sometimes are found at considerable distances from streams, which may be the reason for the modification in the statement by Arrington, who says only that "the location

must be exposed to the hot southwestern sun, and the sand must be slightly, but only slightly, moist to insure proper incubation."

Ditmars adds that Ralston had several captive specimens lay eggs, half of which were placed in damp sand and the other half buried in dry sand, in both instances exposed to sunlight. Those in dry sand shriveled and became desiccated, whereas those in damp sand hatched within a period of 28 to 30 days. Arrington (*supra cit.*) gives the period of incubation as 30 days.

Concluding his account, Ditmars states that Ralston informed him that freshly laid eggs contained "minute but well-formed embryos," and the same statement is paraphrased by Arrington, although earlier, in 1904, Ditmars himself had observed that four eggs laid by a captive, although fertile, were "in such a primary state of development that they contained nothing but a germinating spot to represent the future embryo." Eggs laid by the captive obtained in 1952 from Dr. C. H. Lowe were examined shortly after oviposition, and, while it is not certain that they were fertile, there was no sign of any embryo. While other lizards, notably *Sceloporus clarki*, inhabiting the region occupied by *H. suspectum* are definitely known to deposit eggs with the embryo already well developed, Ralston's statement concerning the eggs of the Gila monster remains to be substantiated. Indeed, the number of days that he gives as the time required for the incubation of the eggs seems abnormally short and verification is desirable before it can be accepted.

SIZE OF HATCHLING

Ditmars says that the hatchling of *H. suspectum* is of "stout appearance and about four inches [102 mm.] long." Arrington (1930) says that "husky three and a half inch [88 mm.] lizards dig their way out," although he does not indicate that this statement is based on his own observations. Neither Arrington nor Ditmars indicates whether the measurements given represent the total length or the body length. However, Cuesta Terrón (1930) makes a more precise statement and notes that "*los escorpiones nacen delgados y como de 12 cms. de longitud total*," ostensibly referring to *H. horridum*. Thus he ascribes to the hatchling

of the larger species a total length of approximately 120 mm., but says that the hatchling is slender rather than "husky" or "stout."

In view of the fact that no specimens are extant to confirm any of these statements, all of them are to be considered extremely rough approximations. The smallest specimens we have examined may not have been captured immediately after emergence, but it seems probable that these more closely approach the actual dimensions of the hatchling. The smallest specimen of *H. suspectum*, from north of Globe, Arizona, in the region of intergradation between *suspectum* and *cinctum*, has an over-all length of 170 mm., with a body (snout to vent) 120 mm. long. The smallest example of *H. horridum*, a specimen of the nominate race from Montaña de la Gloria, at the Isthmus of Tehuantepec in Oaxaca, México, is 204 mm. in total length, with a snout-to-vent length of 120 mm. While *horridum* has a longer tail, it is of interest to note that this small juvenile has a body length identical with that of the smallest *suspectum*.

SEX RATIOS

Preserved specimens provide the only source of information concerning the representation of the sexes in the species and subspecies of *Heloderma*. Data derived from such samples do not necessarily reflect with accuracy the composition of the populations in nature. It is manifest that samples obtained by the collector are often biased, most often perhaps as a result of differences in the behavior of the male and female of any given species. The female may be more secretive than the male, particularly at some season in the year. Or, of even greater biological importance, as a result of such differences in habits or differences in size, there may be a differential survival of individuals of the two sexes, even though it is usually difficult to obtain data that actually substantiate such an assumption. More often it is impossible to offer any good explanation for the composition of the samples representing a species or subspecies. This is true of *Heloderma*, quite aside from the fact that samples for some populations are obviously too small to permit us to draw reliable conclusions.

As noted elsewhere in the present paper, we have found no marked differences between the

sexes in any population of *Heloderma*, nor for that matter have we discovered any reliable method of distinguishing the male from the female except by dissection. Moreover, there is no differentiation that can be detected by gross examination in the gonads of juveniles. In the samples representing each of the five races, the smallest specimen in which the gonads could be identified as either ovary or testis had the following snout-to-vent dimensions: *cinctum*, 227 mm.; *suspectum*, 227 mm.; *exasperatum*, 220 mm.; *horridum*, 169 mm.; *alvarezi*, 143 mm. These figures are not particularly significant in view of the fact that

17 mm.; variations may probably be attributed, at least in part, to the season of the year when the specimens were preserved. In adult females the ovaries vary in their greatest dimensions from 16 to 29 mm., depending largely upon whether ripening eggs are present; in such specimens the oviducts are thick-walled and well developed.

When eviscerated specimens, juveniles, and other individuals poorly preserved or otherwise unsuitable for satisfactory examination are excluded, the few data obtained can be tabulated, with the races arranged from north to south, as follows:

	MALES	FEMALES	RATIO
<i>H. s. cinctum</i>	16	6	2.7/1
<i>H. s. suspectum</i>	29	41	1/1.4
<i>H. h. exasperatum</i>	10	5	2/1
<i>H. h. horridum</i>	15	7	2.1/1
<i>H. h. alvarezi</i>	2	4	1/2
Totals	45	47	1/1.04

few juveniles are available in the samples representing *alvarezi* and *cinctum*, and no juveniles at all in the sample of *exasperatum*. Immature specimens, those with snout-to-vent length between 245 mm. to 260 mm., usually have small but recognizable testes or ovaries, although in females the oviducts are not thickened or well developed. In males presumed to be sexually mature the testes vary in length from 8 to

It is apparent that males outnumber the females, except in the small sample representing *alvarezi* and in the comparatively large sample representing *suspectum*. However, in the entire sample, for the genus as a whole, the ratio of males to females closely approximates one to one, and it is far from certain that differences between the samples have any real biological significance.

GROWTH AND LONGEVITY

Klauber (1937) has discussed the problems concerned with ontogenetic changes, sexual dimorphism, and other phenomena associated with growth in rattlesnakes. Furthermore, he has demonstrated that considerable information regarding these phenomena can be obtained by studies of suitably large series of preserved specimens. Unfortunately the requisite samples are not available for comparable studies of the lizards of the genus *Heloderma*. Such tentative inferences as can be drawn from the limited samples can be found in the taxonomic section of this paper under the discussions of variation within the samples representing each of the five subspecies. The data

need not be repeated here, but it will suffice to note that they point to the probability that relatively minor changes occur during the post-natal ontogeny, the tail and the claws becoming proportionately longer in the adult, while the head tends to become broader in proportion to length. In general adult males tend to have broader heads and longer tails than adult females, but there is no sharply defined difference between the sexes. Boulenger with only two specimens of *suspectum* (1891a) indicates that the neural spines of the vertebrae are better developed in males than in females. This statement is borne out by our examination of additional skeletons, although the differences

are not so pronounced as Boulenger's figure indicates.

GROWTH

Few records have been kept of the growth, and those available all refer to *H. suspectum*. One of these was an adult and the other apparently a subadult, both kept under the abnormal conditions of captivity. Durham (1951) reports that a captive taken near Hermosillo, Sonora, México, had a total length of 400 mm. on July 26, approximately two months after it was caught. On November 23 of the following year, nearly 16 months later, after losing 297 grams in weight during the preceding 11 months, it measured 420 mm., having increased but 2 cm. in length. It seems doubtful whether the measurements were precise, however, as Durham's figures indicate that between October, 1946, and November, 1947, the specimen had decreased 4 mm. in total length, probably attributable to error as the result of the difficulties experienced in obtaining measurements.

We are indebted to Mr. Roger Conant for information concerning a small specimen from 15 miles northwest of Lordsburg, New Mexico, that was obtained by the Philadelphia Zoological Garden in 1951. When measurements were obtained on May 31, 1951, it had an over-all length of 400 mm., and a snout-to-vent length of 277 mm. It still had many features of the pattern characteristic of juvenile *H. s. suspectum*, although it was larger than most juveniles. On February 17, 1953, when Mr. Conant generously obtained measurements, it had attained an over-all length of 489 mm. and a snout-to-vent length of 338 mm. Thus during a period of approximately 21 months it had gained 89 mm. in over-all length, or 22 per cent of its total length when first measured.

Woodson (1948) briefly reports the observations of Charles A. Hewitt, who kept three Gila monsters in captivity in Buena Park, California, stating only that "his conclusion is that they grow slowly, his showing an average yearly increase of about .47 inch [*ca.* 11 mm.]." In correspondence Mr. Hewitt informs us that one Gila monster obtained on March 28, 1938, was 19 inches in over-all length, and when last measured on November 14, 1948, over 10 years later, it had reached a length of 21.75 inches. As this was an exceptionally large specimen,

with the maximum length known to be attained by the species, it seems evident that under favorable conditions growth may continue after adult dimensions have been attained. A gain in length of 2.75 inches (70 mm.) over a 10-year period indicates an average yearly increase approximating 7 mm.

Despite the lack of satisfactory data, there can be little doubt that growth in the hatchling proceeds at a considerably faster rate. The graph (fig. 12) employed primarily to show the relationship of body length to tail length will also serve to illustrate the distribution by size of the samples representing the two species. It can be seen that the majority of the juveniles of both species fall between the limits of 130 mm. and 160 mm. in snout-to-vent length. It seems probable that such specimens are in their first year of life. Individuals with body lengths between 160 mm. and 210 mm. evidently are not commonly collected, as there is but one specimen of each species in the series measured. There is no simple means of finding out whether growth occurs during the period of hibernation at the close of the first growing season, whether these lizards are merely more secretive, or whether there is a high mortality during the first year, but it seems probable that individuals of both species are approaching sexual maturity during their second year, as indicated by an examination of the gonads, which are undifferentiated in the hatchling.

In figure 12 it can be seen that there are three specimens of *H. horridum* that fall in the neighborhood of 215 and 220 mm. While it is not indicated on the graph, where the data for various races are not plotted by separate symbols, these three half-grown members of the species chance to represent, respectively, the three subspecies, *horridum*, *exasperatum*, and *alvarezi*. Furthermore each of the three specimens possesses pattern characters that are intermediate between those of the juvenile and those of the adult. Such specimens are almost certainly in their second year. It may be inferred that few specimens between 220 and 300 mm. are encountered in the field. During their third year of life most individuals of the species would seem to have attained a snout-to-vent length of roughly 300 mm. Thereafter growth presumably occurs at a slower but more

or less continuous rate, until maximum size is attained.

As far as the sample of *suspectum* is concerned, there is no indication of any grouping of individuals between the second and third years. It is possible that individuals 225 mm. in body length are in their second year of life. Thereafter variations in the growth of individual specimens, at least when specimens from the several areas throughout the entire range are plotted together, obliterate any distinction that might exist between the curves that conceivably could be plotted for animals respectively in their second and third years, were there any simple means of establishing the age of individuals. The graph (fig. 12) suggests that Gila monsters normally reach a maximum size of approximately 325 mm. in body length that is exceeded only by exceptional individuals.

The inferences that can be drawn from such data may not be wholly reliable, but it is noteworthy that the majority of North American reptiles thus far studied fall into a somewhat similar growth pattern. In fact, the histogram provided by Klauber (1937, fig. 4) to show the distribution of the size classes in a series of 858 rattlesnakes of the same species obtained during a single year at Plateville, Colorado, provides a picture of the pattern of growth in a homogeneous population that is not dissimilar from that less adequately shown for the two species of *Heloderma*.

LONGEVITY

The Gila monster as well as the Mexican *escorpión* is relatively hardy and most, but not all, individuals are easily fed under captive conditions. Also, by virtue of their large size, their venomous qualities, and the fact that they are not difficult to obtain, these lizards are commonly exhibited in zoological gardens, especially in the United States. *Heloderma horridum* is not so frequently obtained and seems

to be less easily maintained than *suspectum* under captive conditions. Flower (1937) states that as far as he could ascertain, no specimen of *horridum* had been exhibited in Europe. However, 10 Gila monsters kept in London had survived for an average of almost nine years, and one had lived there for 17 years, eight months, and four days. Mann (1930), however, gives 19 years and four months as the maximum life span authenticated for *suspectum*. In contrast the longevity record for *horridum* is given by Mann as three years and three months, but the animal was still alive at the time he wrote. More recently Conant and Hudson (1949) report longevity records of nine years for *H. horridum*¹ and 20 years for *suspectum*. Señor Alvarez del Toro informs us that a specimen of *H. h. alvarezi* still alive in the zoo at Tuxtla Gutiérrez, México, in 1950 had been there for eight years.

This longevity record for the Gila monster is equaled or bettered by that of an Australian skink, *Egernia cunninghami*, and by two European anguids, namely, *Ophisaurus apodus*, which have attained a maximum of 24 years (Perkins, 1947), and *Anguis fragilis*, the oldest lizard on Flower's (1937) list, with a known life span of 32 years. Such records are partly to be ascribed to the adaptability of these lizards to captive conditions, and they do not, of course, offer conclusive proof that under natural conditions greater ages are not attained by lizards of other families.

¹In a letter dated April 7, 1955, Mr. Charles E. Shaw of the Zoological Society of San Diego informs us that a specimen of *H. h. horridum* was received from Mr. Charles A. Hewitt on December 17, 1949. Mr. Hewitt obtained it on October 6, 1944, from a dealer who claimed that it had been captured on October 25, 1942, "on desert near Mexico City." The source, and probably the date of capture as well, are open to question, but there is no question that the specimen has been in captivity for at least 10 years and seven months. Thus it is older than any other reported, and, as it was still living when Shaw wrote in 1955, it will establish a new longevity record.

ECOLOGY

HELODERMATIDS, as have nearly all other animals, have become more or less specialized for life in a narrow range of environmental conditions. By being so specialized they can be more efficient. This, of course, does not imply that helodermatids are able to cope efficiently with all the hazards of survival that exist in the regions they inhabit. Rather it implies a fair degree of specialization primarily for particular climatic and physical factors; secondarily, the lizards are specialized in their food and feeding habits as well as in the ways they defend themselves from enemies.

Habitats are described for each of the subspecies in the taxonomic section, and other aspects of their ecology are discussed, often from other standpoints, to be sure, in the sections dealing with clines, food and feeding habits, fat storage, activities, and other aspects

of their behavior. In this section we discuss such environmental factors as heat and moisture in an effort to show how these factors affect the distribution and activities of helodermatids. Also we point out their more obvious adaptations for survival, including their avoidance of enemies and their means of defense.

The information concerning many aspects of the ecology of *Heloderma* is fragmentary, and much of what is now in print is anecdotal or the result of casual observation. We have carried out limited tests under laboratory conditions, but much pertinent information can be obtained only when it is possible for someone to carry out prolonged studies under field conditions with marked animals. Such a project, to be productive, might require several years.

THERMOREGULATION AND HEAT REQUIREMENTS

Despite the fact that both species of *Heloderma* inhabit relatively warm regions they are not thermophilic as compared with many other lizards. The Gila monster and the *escorpión* are not wholly nocturnal in habits, but diurnal activity is largely restricted to cooler periods, during or following rains, or when the sky is overcast. Shufeldt (1890) states that the Gila monster is "very fond of basking in the hottest of noon-day suns." In contrast Arrington (1930) reports that during the month of April two individuals exposed to the sun at 9:30 A.M. at Tucson, Arizona, were found dead an hour later. Arrington notes that on warm days captives liberated in the sun immediately seek any bit of shade available.

Few reptiles inhabiting deserts can withstand prolonged exposure to temperatures greatly exceeding 40° C., even though some iguanids and teiids are not infrequently abroad with body temperatures momentarily at such levels (Cowles and Bogert, 1944). However, iguanids and such teiids as *Cnemidophorus* are diurnal lizards that habitually bask, in contrast to *Heloderma*, which if it basks at all under natural conditions probably resorts to this method of raising its body temperature only during relatively cold weather. There are no reports

of Gila monsters basking except under captive conditions.

NORMAL ACTIVITY RANGE

The range of body temperatures that any species of lizard will voluntarily tolerate can be ascertained by either of two methods. When individuals are abundant in their native habitat the temperature of each of a sufficiently large number to provide an adequate sample can be recorded immediately after capture (Bogert, 1949a). However, this method is impractical for studies of species infrequently encountered in the field. An alternate procedure requires the use of but one or a few live individuals, which must be maintained in a suitably large cage or enclosure provided with one or more sources of radiant heat. Ordinary commercial heat lamps serve the purpose. Heat is provided at one end of the cage, while the other end is allowed to remain at room temperature or cooled if need be. Under such conditions the lizard can either seek heat or avoid it, if it is allowed to move freely in the enclosure. The lizard can be seized and its body temperature can be recorded at intervals.

The cage used to ascertain the normal activity range, as defined by Cowles and Bogert

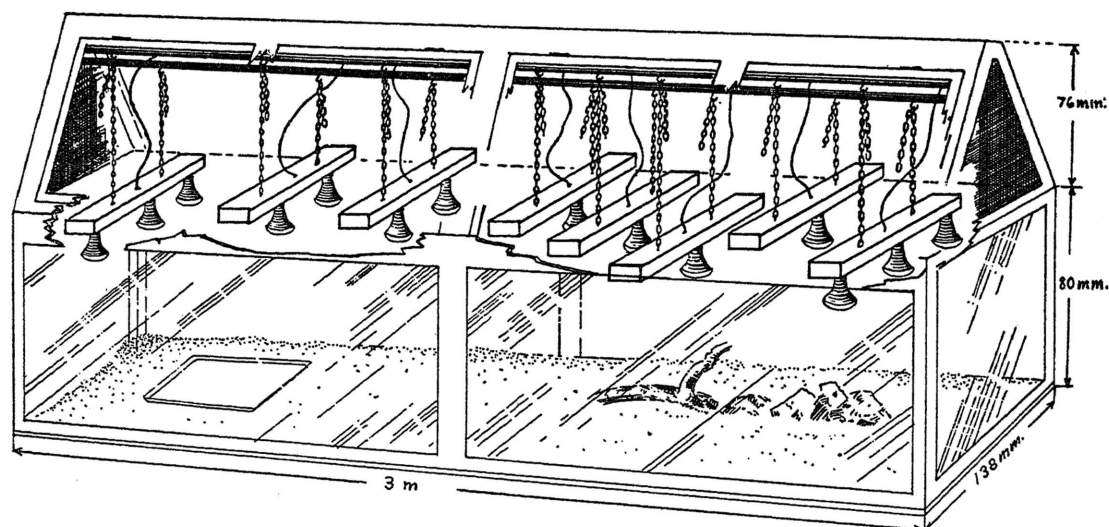


FIG. 32. Diagrammatic view of the cage, employed to ascertain the normal activity range in body temperatures of the Gila monster, with adjustable heat lamps providing sources of radiant heat. Fluorescent lights, not shown in the diagram, provided light. Each row of lights operates from a separate switch, with five sockets available in each row.

(1944), is depicted in figure 32, where dimensions of the enclosure are indicated. Heat lamps were suspended from the top of the cage by means of chains so that five heat lamps in each row could be raised, lowered, or shifted laterally, depending upon requirements. The floor of the cage was provided with a layer of sand varying in depth from 5 to 10 cm. A few rocks and sheets of slate were deposited on the sand in order to provide suitable retreats for the Gila monsters when they were inactive. Ordinarily three 250-watt heat lamps were suspended at a height of approximately 50 cm. above the surface of the sand at one end of the cage. Two additional lamps were suspended at a somewhat higher level 45 cm. to the left, with one additional heat lamp still higher above the sand near the middle of the cage.

The left half of the cage was not provided with heat lamps, while the Gila monsters were being tested, although ordinary light bulbs were inserted in some sockets to produce approximately the same amount of illumination in the unheated half as in the other half of the cage. Fluorescent lights, not shown in the diagram, were placed on the inner edge of each side of the cage approximately 75 cm. above the floor to provide additional illumination. The sides of the cage were of glass, but the top was screened to allow for the loss of heat by convection from the sand on the bottom of the cage.

Contrary to such assumptions as those of Herter (1940a, 1940b, 1941), who employed a carefully controlled gradient in the temperature of the substratum but failed to record body temperatures, it is not necessary to use an apparatus with a temperature gradient in order to allow reptiles to regulate their heat intake. Reptiles absorb heat from the substratum or directly from solar radiation when abroad during the day. To a limited extent there may be a transfer of heat by convection or conduction to or from the surrounding atmosphere. Under natural conditions reptiles avail themselves of different thermal levels in both time and space to avoid extreme temperatures. If suitable conditions are provided under laboratory conditions, reptiles maintain the thermal level of the body at a mean level that is characteristic of the species. As pointed out by Bogert (1949a), two species of lizard may be found side by side in the same habitat, yet one lizard may have a mean body temperature 5°C . or 6°C . higher than that of the other, with relatively little overlap in the ranges of body temperature voluntarily tolerated. In a cage provided with heat lamps at one end, reptiles of different species have maintained the body at mean thermal levels that differed by as much as 15°C .

It may be questioned whether lizards react to changes in their body temperature as efficiently in the laboratory as they do in their

native habitats. In order to ascertain whether they so react, means calculated for series of temperature records secured in the laboratory have been compared with means for series obtained by shooting lizards under field conditions and recording their body temperatures immediately afterward. For example, means for three series of the same species of lizard were obtained. One series was obtained during the winter months (in the Bahamas). A second series was obtained on the same island during the summer, and a third series was obtained from 20 specimens kept in the same cage as that employed in our study of the Gila monster. Despite differences in air temperatures in summer, winter, and in the laboratory cage, there was no significant difference between the three means for body temperatures obtained; they differed by only 0.2°C . There is, therefore, considerable reason to believe that means and extremes recorded for the Gila monster in the laboratory cage would agree with those that might be recorded under actual field conditions.

Three Gila monsters were employed in our tests. All came from Pima County, Arizona. The largest of the three (No. 1), taken on the outskirts of Tucson, had been in captivity for over a decade prior to its use in the tests. The other two, one (No. 2) from near Tucson, and one from Quijotoa (No. 3) that was exceedingly thin and emaciated when captured, were taken during the previous summer. Tests were undertaken early in March when the first signs of activity were noted in the three animals. All had been relatively dormant during the winter,

prowling about the cage, while the other two remained under the rocks provided for shelter. The greater activity of the emaciated individual can probably be attributed to the stimulus produced by its hunger.

The number of times the body temperature of each individual was recorded provides a rough index to its activity in view of the fact that records were made at random intervals, when any individual found abroad in the cage was seized. No. 1, which had been supplied with adequate food during its long period in captivity, was active about half as often as No. 2, which to judge from the diameter of its tail had stored a moderate amount of adipose tissue prior to its capture. In contrast, the thin individual, No. 3, was approximately four times as active as No. 1, and twice as active as No. 2. It is possibly significant that the maximum as well as the minimum body temperatures obtained in the tests were for No. 3, which was actively digging at 24.2°C . and 33.7°C . While it is possible that these extremes are largely a reflection of the greater number of records obtained for the individual, it seems probable that the hunger drive provided for additional stimulus that led No. 3 to be foraging at body temperatures that the other, less undernourished, individuals avoided. The data derived from all three can be combined to compute a mean value of 27.7°C . Presumably this mean closely approximates what might be obtained from field records. The data from each of the three are tabulated below to show the minor differences manifested in their thermoregulatory behavior:

ANIMAL	NO. OF OBSERVATIONS	MEAN BODY TEMPERATURES IN DEGREES CENTIGRADE	EXTREME BODY TEMPERATURES IN DEGREES CENTIGRADE
No. 1	8	30.1°	27.3–31.9°
No. 2	16	29.3	25.5–32.6
No. 3	33	28.9	24.2–33.7

even though radiant heat had been supplied in the cage they occupied. Tests were continued until June and thus covered a four-month period.

It is noteworthy that the emaciated specimen, which evidently had relatively little fat stored in its tissues, was the most active of the three. This individual was frequently digging or

The data for the three have been combined in the histogram (fig. 33), where it is shown that the mode falls between 29°C . and 30°C ., with over half of the records falling between 28°C . and 31°C ., an approximation of the optimum for normal activities. However, it should not be assumed that the Gila monster will thrive if the body temperature is main-

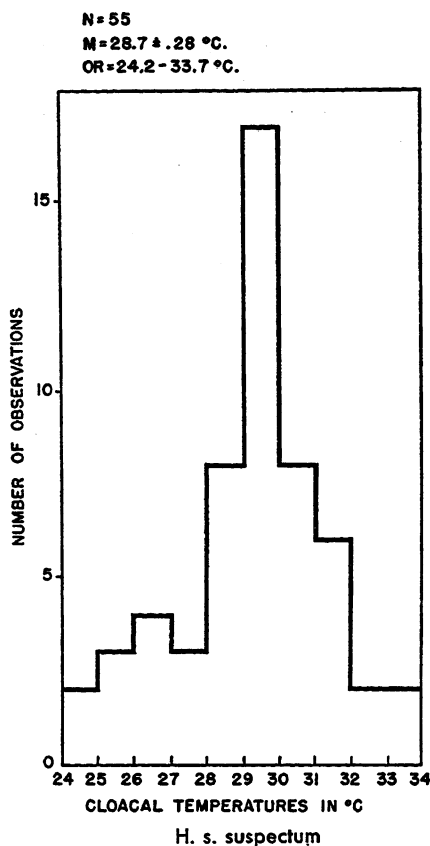


FIG. 33. Histogram showing distribution of body (cloacal) temperatures recorded for three Gila monsters maintained under conditions in the laboratory where sources of radiant heat permitted them to regulate the thermal level of the body by means of their movements. Under such conditions there was a tendency for the lizards to maintain the body at a level closely approximating the mean of the normal activity range.

tained within this range. No precise data are available for *Heloderma*, but when inactive or in such retreats as the burrows that are sought for shelter under natural conditions, it is probable that the body temperature is unavoidably permitted to reach lower levels. In other species that have been tested, prolonged exposure to relatively constant body temperatures at the level of the mean for the normal activity range resulted in partial paralysis. In other words, there is evidence that alternate exposure to high and to low temperatures within the range tolerated is a requirement for the maintenance of normal physiological levels.

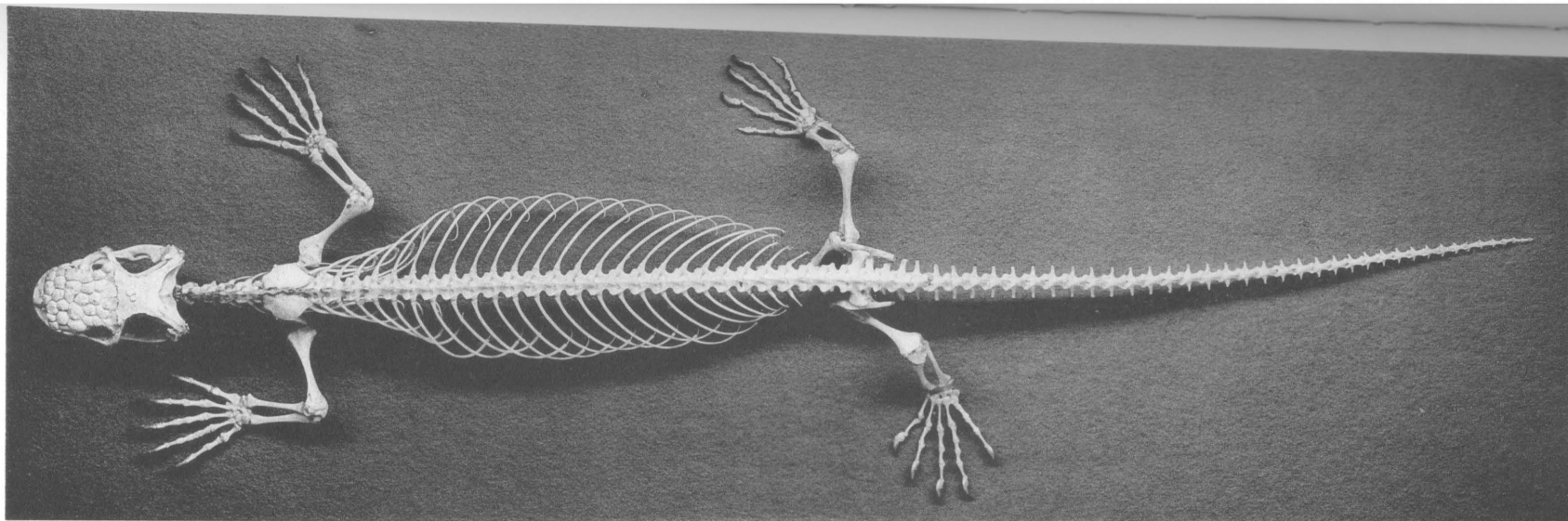
When captured on August 29 at 9:10 p.m. near Cañada del Oro northwest of Tucson, Arizona, a Gila monster had a cloacal temperature of 27.2° C. when the substratum at the point of capture was 31.0° C. on the surface, and the air was 28.2° C. at the level of the lizard. Thus, as often happens with nocturnal desert reptiles, the body temperature was lower than either the air or the substratum, possibly as a result of the lizard's having recently emerged from the cooler depths of its burrow, although there may have been some dissipation of heat as a result of moisture lost to the expired air from the lung surfaces.

Only one live specimen of *H. horridum* has been available to test in the cage provided with radiant heat. This individual was too emaciated at the time it was received to be certain that reliable records could be obtained from it. However, the few temperatures recorded all fell within a degree of the mean for *H. suspectum*, and it seems doubtful whether there are marked differences between the two species in their thermal requirements. This assumption conforms to the conclusions reached in studies of other lizards (Bogert, 1949a, 1949b).

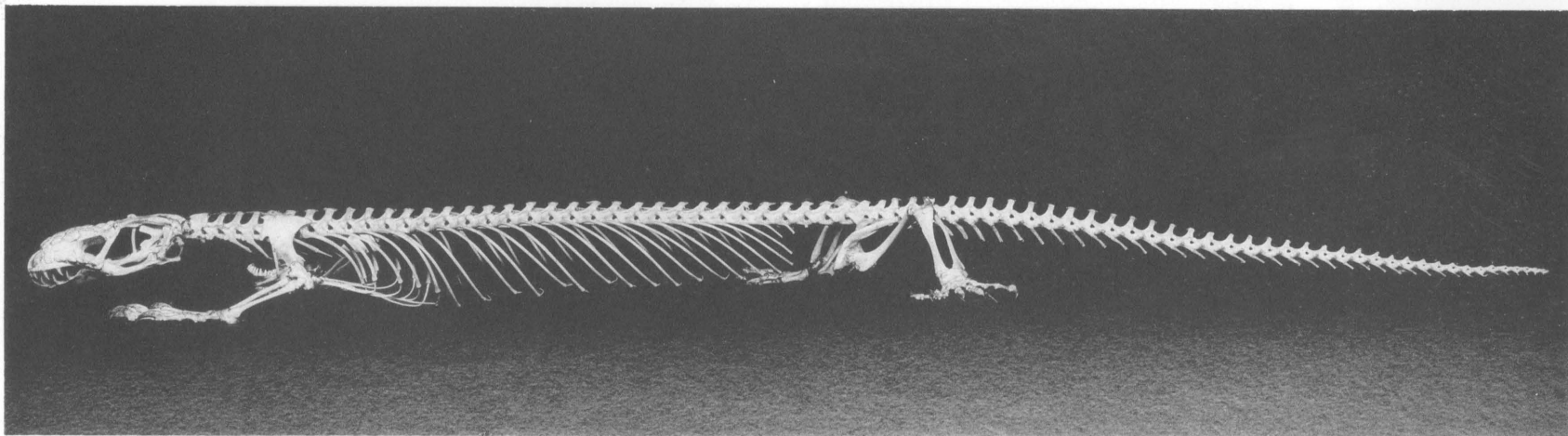
HIGH-TEMPERATURE TOLERANCE

In experiments carried out with reptiles more abundant than *Heloderma suspectum* it has been shown that tolerance to high temperatures is subject to individual variation (unpublished data). When a sufficient number of records are obtained for one species (or even a local population) variations may encompass a range as great as 6° C. Where enough records are available for a curve to be plotted it approximates a normal distribution. Cowles and Bogert (1944) define the critical maximum as "the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death." It should be added, however, that this definition refers to the individual rather than to the species.

In view of the fact that we have but a single record for *Heloderma suspectum*, it has been impossible to ascertain the mean and the extremes of the upper limit of the range of tolerance. A Gila monster weighing 466.7 grams that had been obtained only a few days prior to the experiment was exposed to the direct

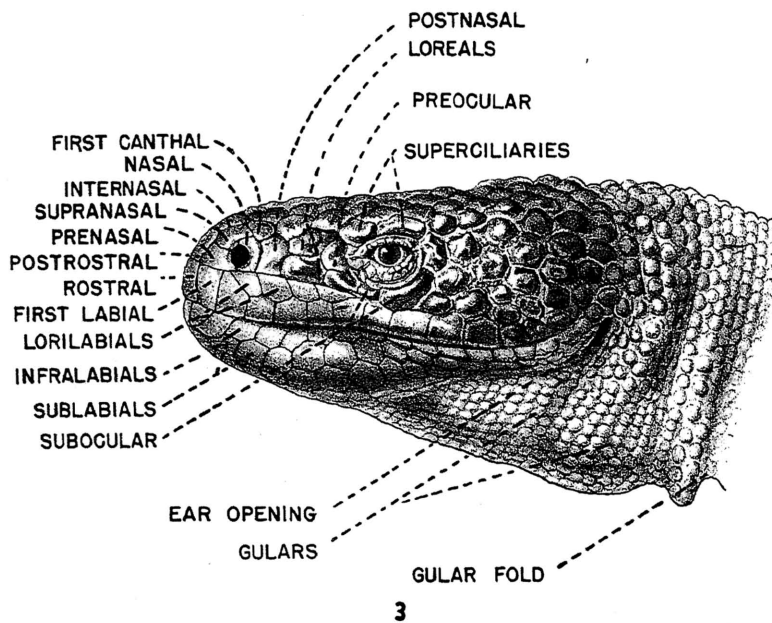
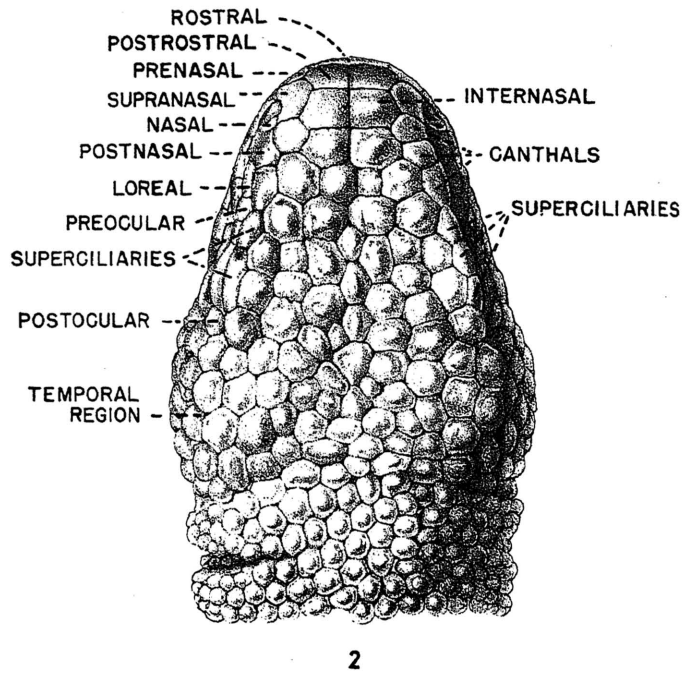
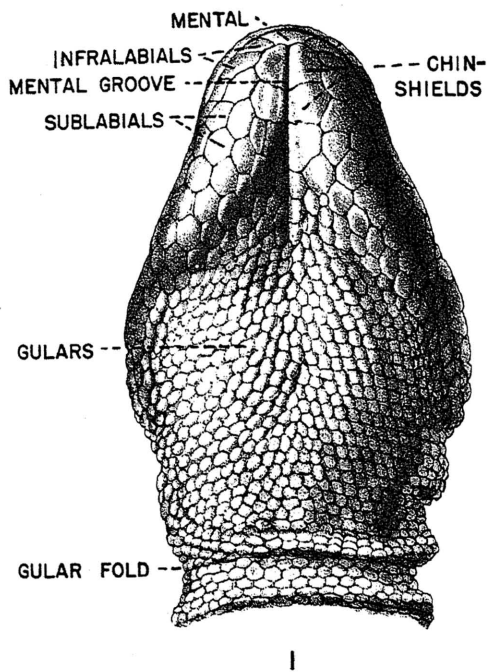


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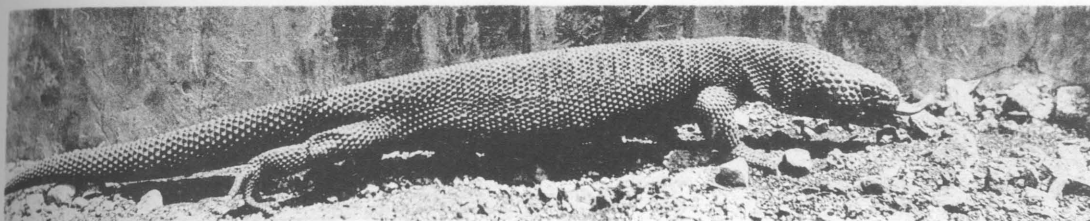


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Complete skeleton of *Heloderma h. horridum*. 1. Dorsal view. 2. Lateral view



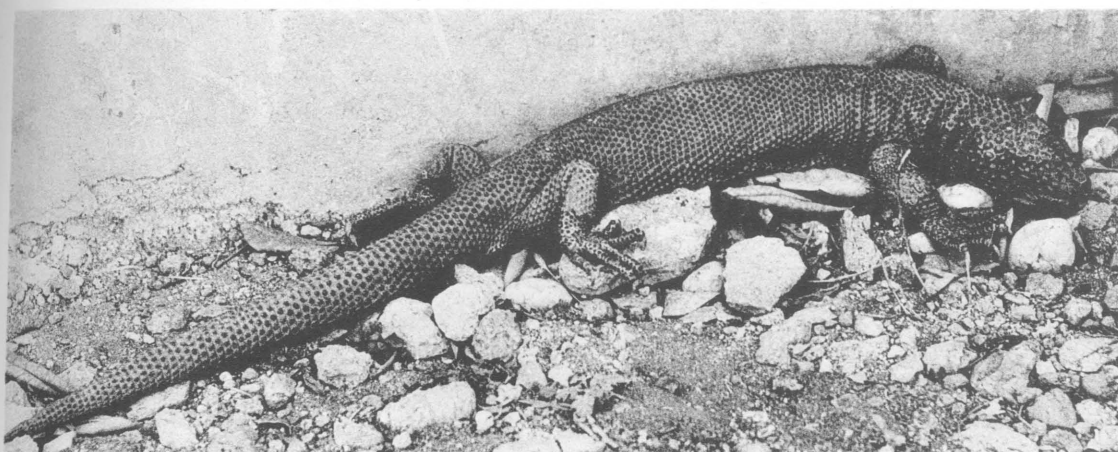
Head of *Heloderma h. horridum*, showing scutellation. 1. Ventral view. 2. Dorsal view. 3. Lateral view. Modified from Duméril, Bocourt, and Mocquart [1874 (1870-1909)]



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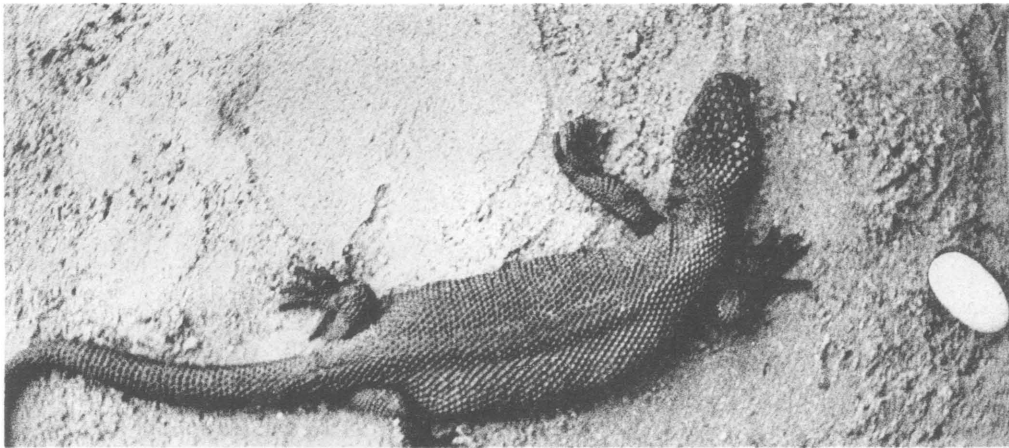


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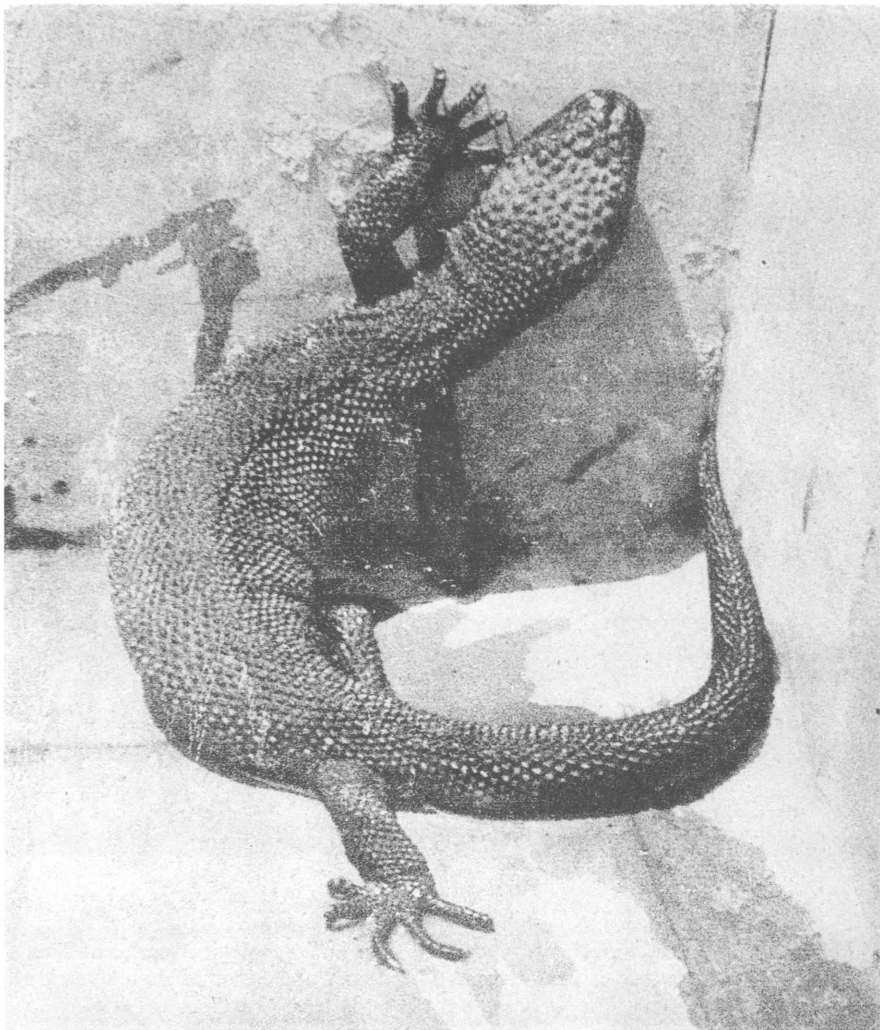


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Three views of *Heloderma horridum alvarezii* paratypes while alive in the zoological garden at Tuxtla Gutiérrez, Chiapas, Mexico. Photographs courtesy of Mr. Thomas McDougall and Señor Miguel Alvarez del Toro



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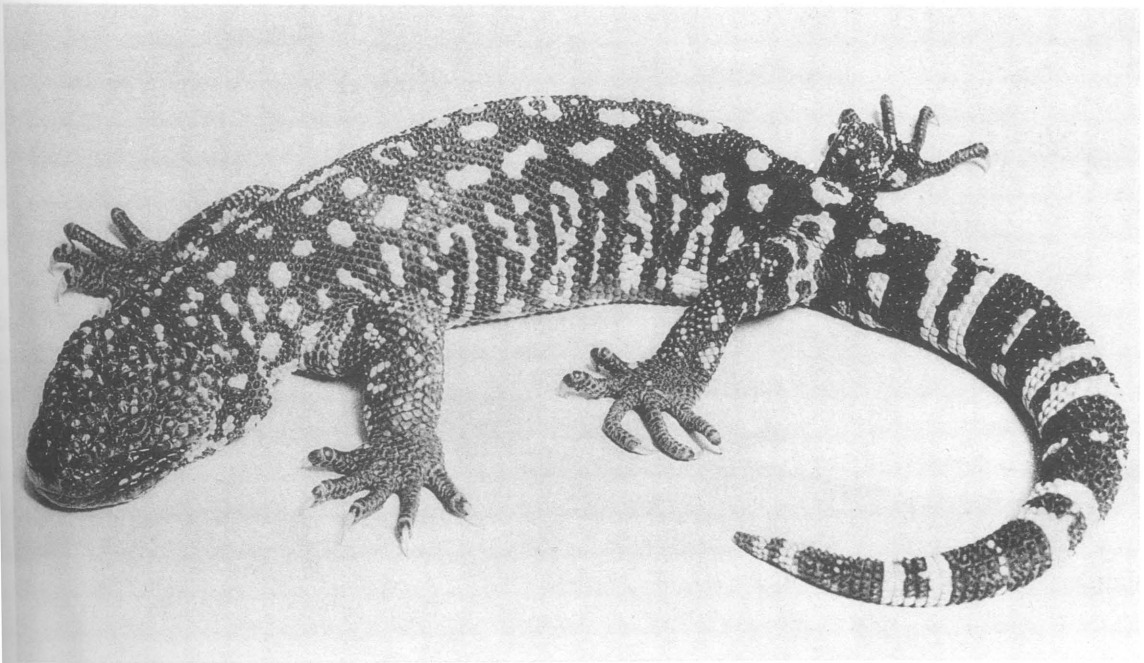
1. *Heloderma horridum alvarezii* with egg deposited while captive in the zoological garden at Tuxtla Gutiérrez, Chiapas, Mexico. Photograph courtesy of Señor Miguel Alvarez del Toro
2. Type specimen of *Heloderma horridum alvarezii* while alive in Mexico City



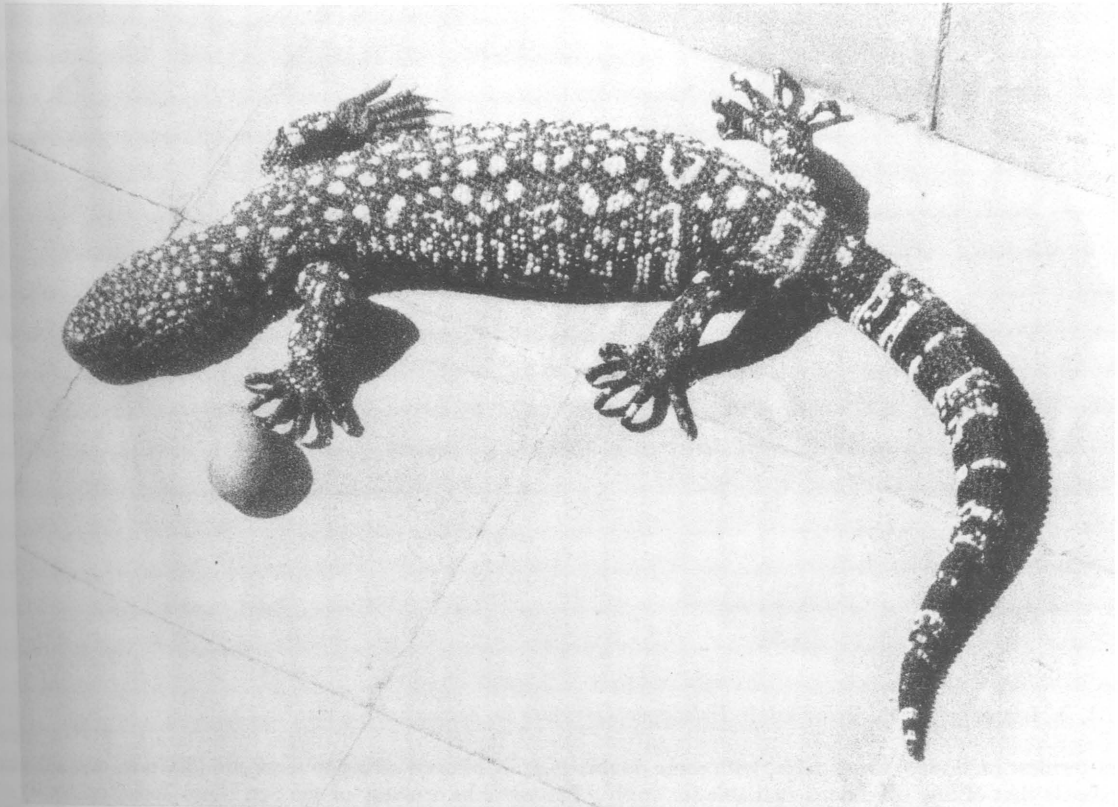
Juvenile of *Heloderma h. horridum* from Tehuantepec, Oaxaca, Mexico, illustrating pattern of hatchling.
1. Dorsal view. 2. Ventral view. 3. Lateral view. Reproduced from color plate in Günther, 1885



Ontogenetic changes in the pattern of *Heloderma h. horridum*. 1. Juvenile from Bisilana. 2. Half-grown individual from La Concepción. 3. Adult from Cerro de Mixtequilla. All in the state of Oaxaca, Mexico

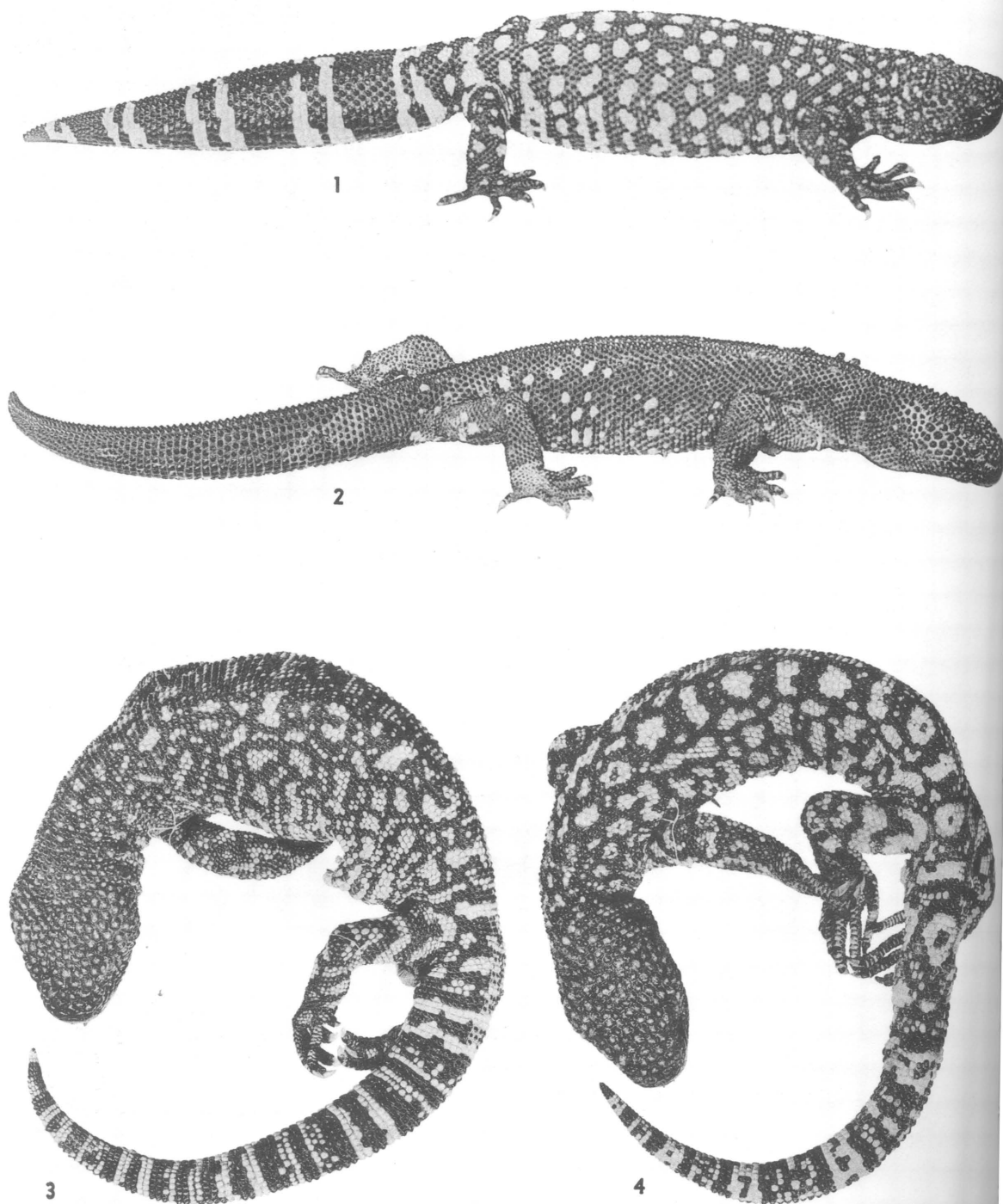


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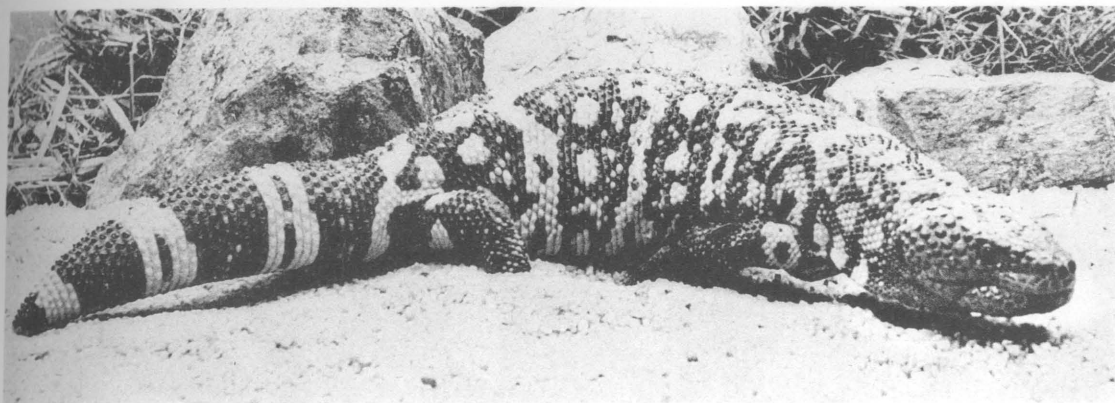


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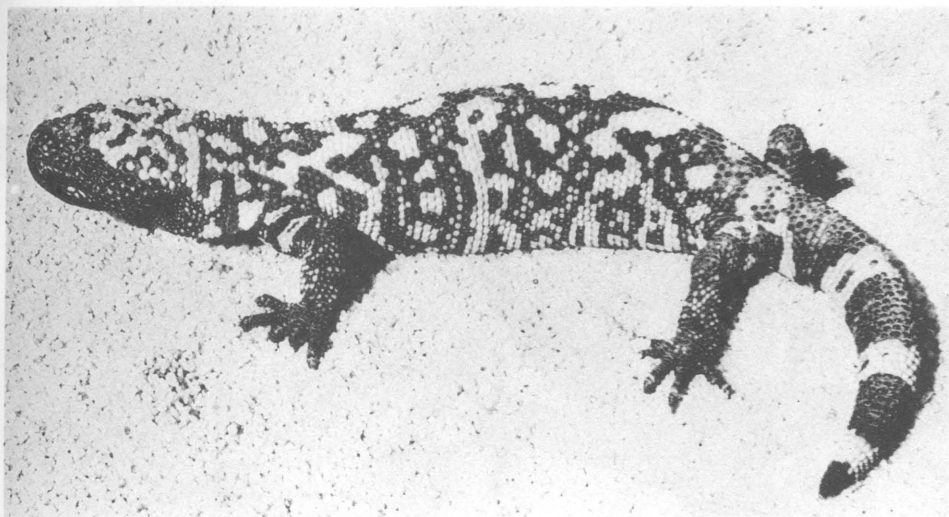
Patterns in adult *Heloderma h. horridum* represented by living specimens. 1. From Canón del Lobo, near Cuernavaca, Morelos. 2. Female from Placeres de Oro, Guerrero, Mexico, with egg, one of 10 laid during November, 1949, while in captivity. Photographs by Edmundo Martín del Campo



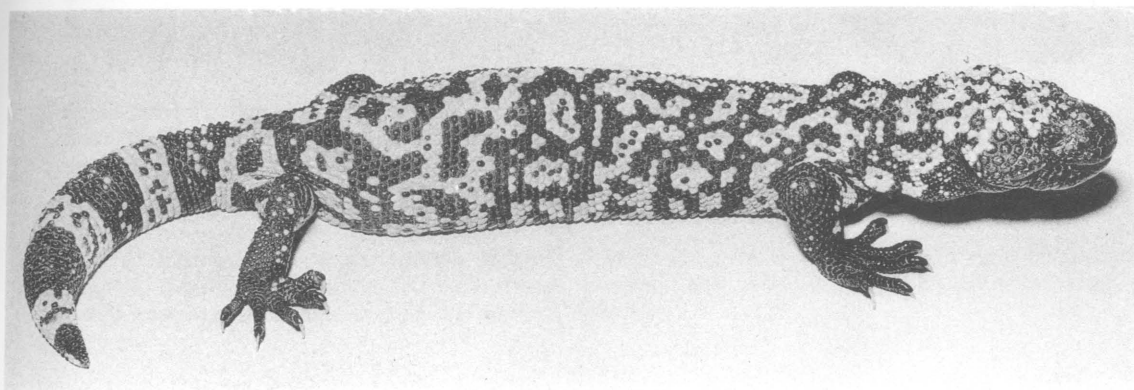
1, 2. Lateral views of living adult *Heloderma horridum* in Zoological Garden in San Diego, California. Source of specimens unknown. 1. Specimen with pattern resembling that of individuals from Oaxaca. 2. Dark, almost patternless individual identifiable, with some doubt, as *H. h. alvarezii* owing to large size (800 mm. over all), which exceeds that of any specimens available for study. Photographs courtesy of the San Diego Zoological Society and Mr. C. H. Shaw. 3, 4. Type and paratype, respectively, of *Heloderma horridum exasperatum*, both from Guirocoba, Sonora, Mexico. Alcoholic specimens in the American Museum of Natural History



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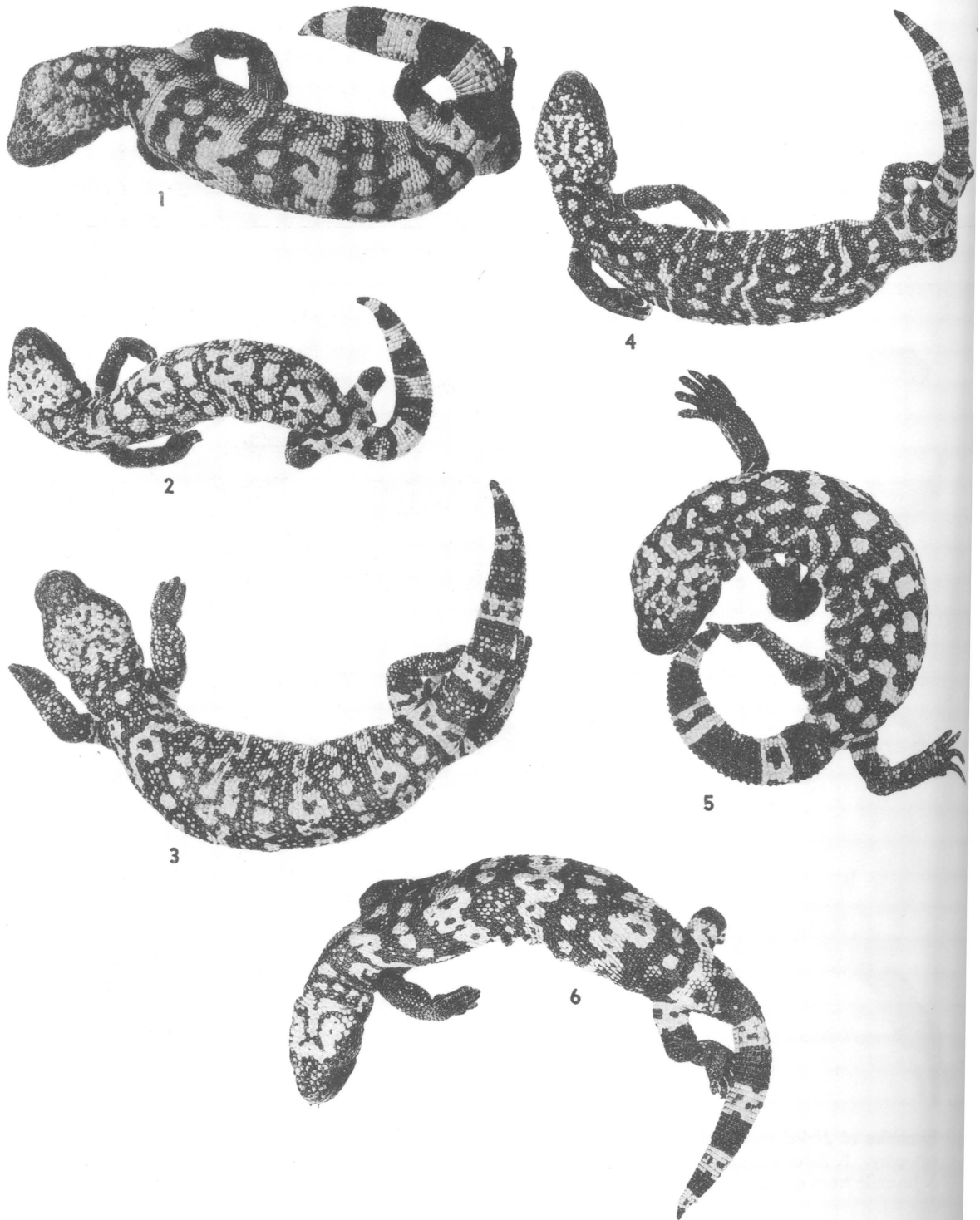
Adult examples of *Heloderma s. suspectum*. 1, 2. From Tucson, Pima County, Arizona. 3. From McGee Mine, Peloncillo Mountains, Hidalgo County, New Mexico; photograph by Isabelle de P. Hunt, courtesy of Mr. Roger Conant



Examples of *Heloderma s. suspectum* to illustrate ontogenetic changes in pattern from simple barred condition of juvenile to mottled, reticulated pattern of adult. 1. Adult from near Tucson, Arizona. 2. Post-juvenile from Tanque Verde Ranch in Pima County, Arizona. 3. Juvenile from near Magdalena, Sonora, Mexico



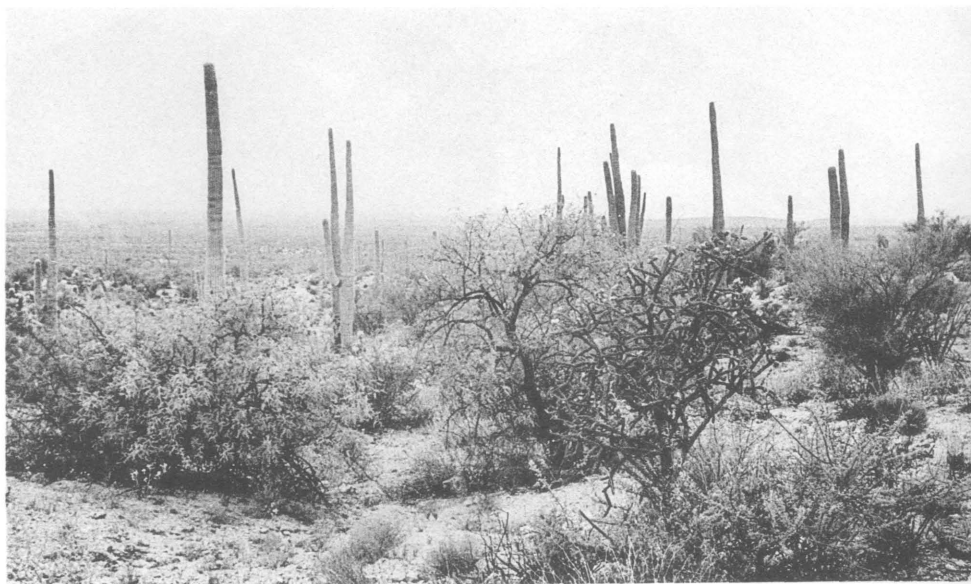
Examples of *Heloderma suspectum cinctum* showing absence of any extensive change in pattern during ontogeny. 1. Adult, type specimen from Las Vegas, Nevada. 2. Post-juvenile from Bloomington, Utah. 3. Juvenile from one-half a mile west of Wickenburg, Arizona



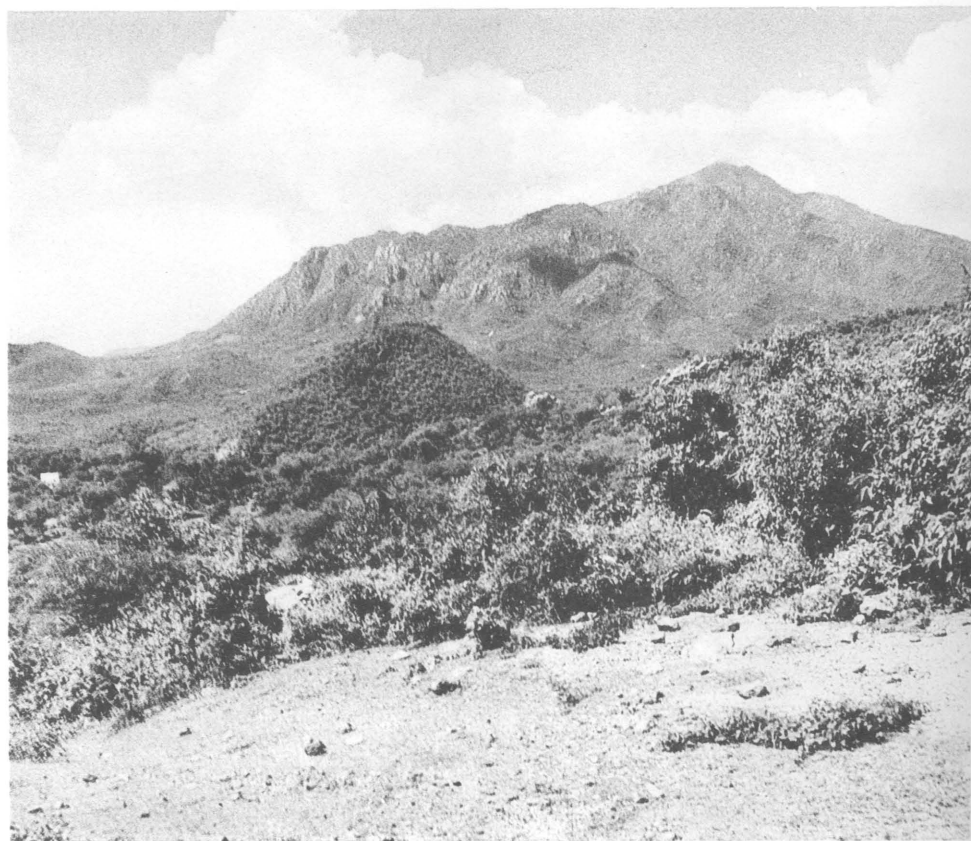
Trends in pattern characteristics in *Heloderma suspectum*, from north to south. 1. *Heloderma s. cinctum*, type, from Las Vegas, Nevada. 2. Pale individual representing northern population of *H. s. suspectum* from 8 miles north of Miami, Gila County, Arizona. 3. Individuals with pattern characteristic of *H. s. suspectum* in Pima County, Arizona. 4. Dark individual of *H. s. suspectum* from Pima County, Arizona. 5. *Heloderma s. suspectum* with coarse reticulum, four broad black bands on tail, representative of population from 5 miles south of Imuris, Sonora, Mexico. 6. Possible intergrade between *H. s. suspectum* and *H. s. cinctum* (see text) from 3 miles south of Aguila, Maricopa County, Arizona, at periphery of range of *H. s. suspectum*



Examples of five subspecies of *Heloderma*, in order of occurrence north to south. 1. *Heloderma s. cinctum* from 2 miles west of Wickenburg, Maricopa County, Arizona. 2. *Heloderma s. suspectum* from 21.5 miles southwest of Tucson, Pima County, Arizona. 3. *Heloderma h. exasperatum* from Guirocoba, Sonora, Mexico. 4. *Heloderma h. horridum* from La Placita, Michoacán, Mexico. 5. *Heloderma h. alvarezi* from Cintalapa, Chiapas, Mexico. Note trend in pattern from light to dark from north to south

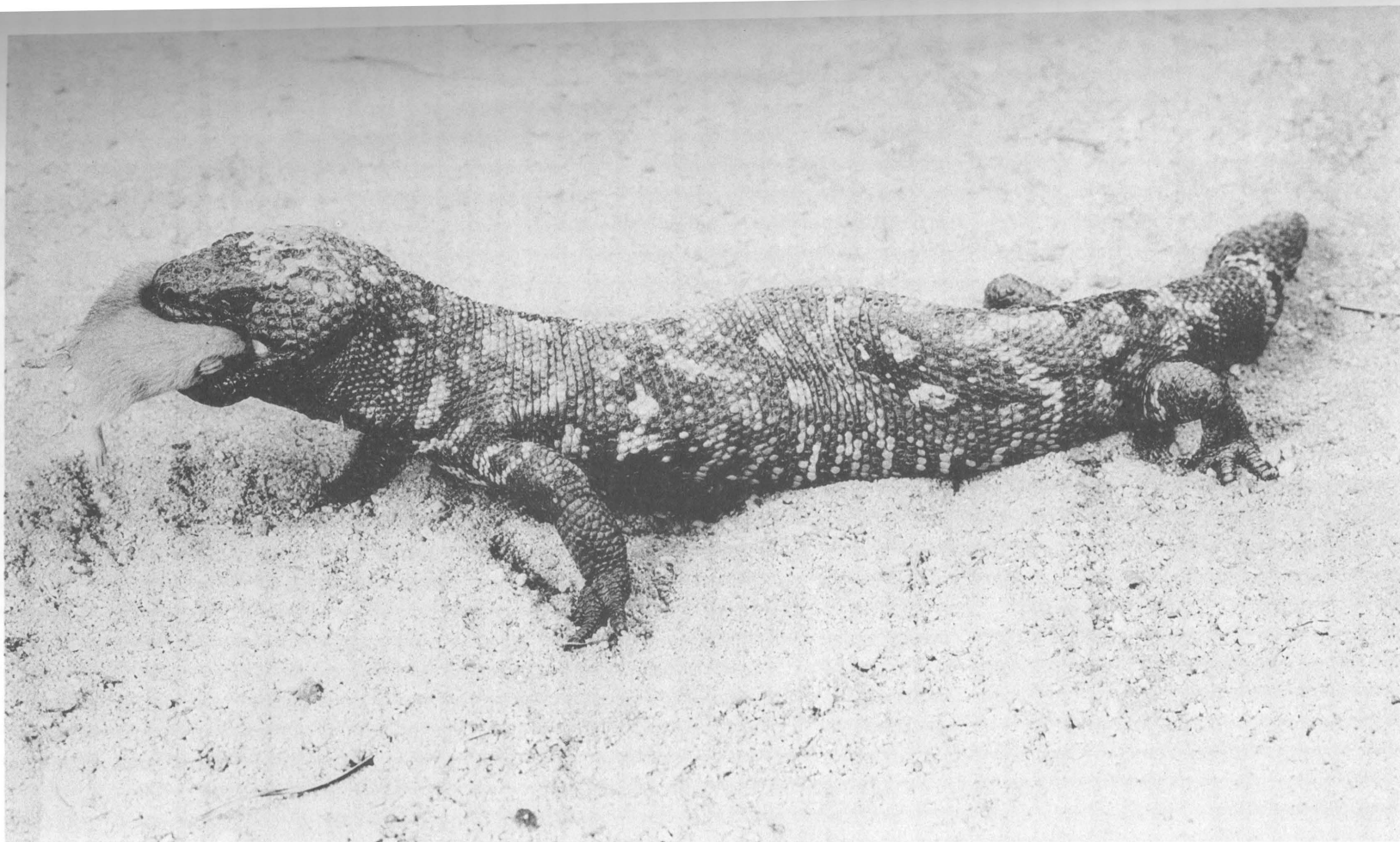


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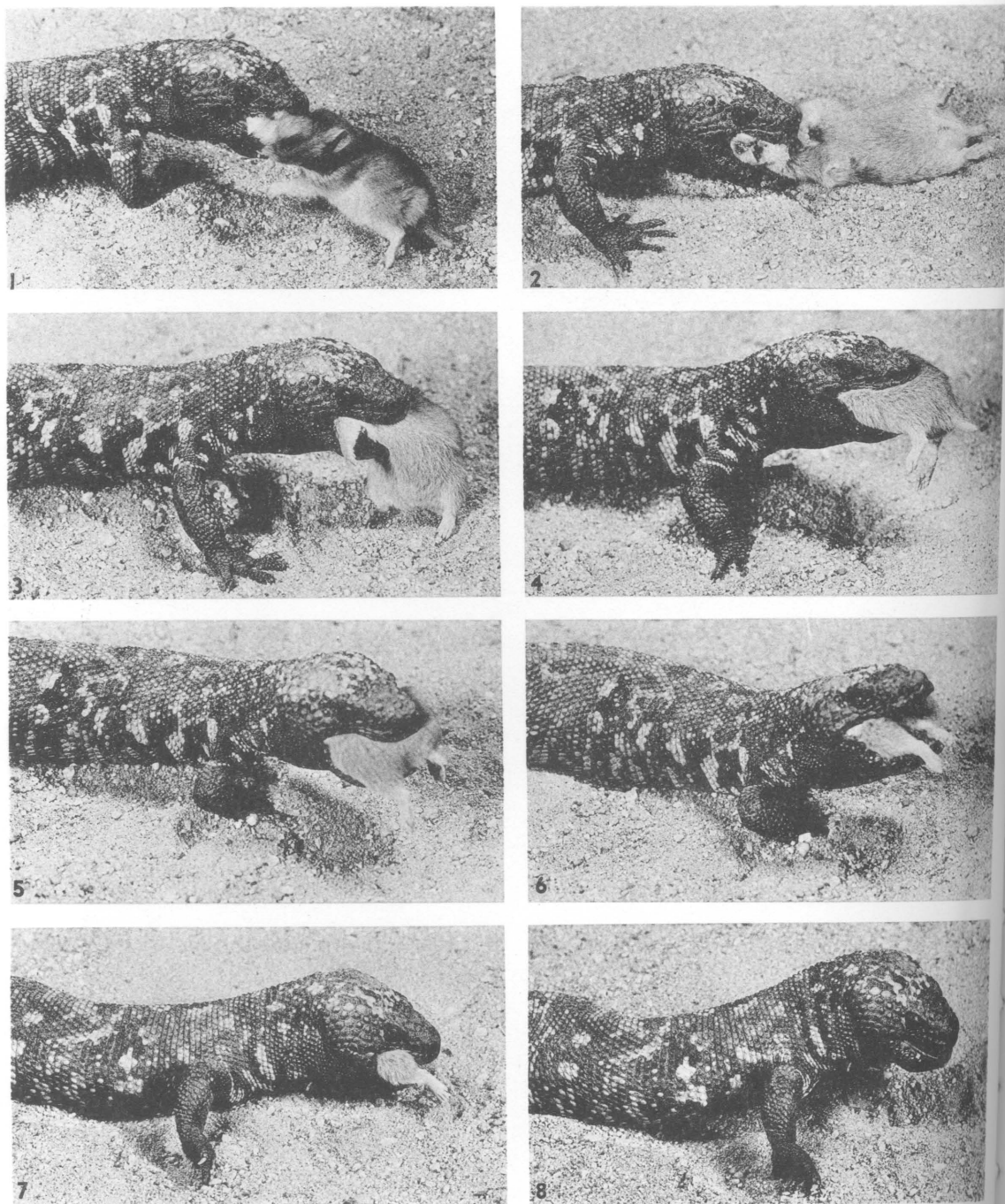


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1. Habitat of *Heloderma s. suspectum* in paloverde-cacti and burr-sage association on alluvial fan of foothills of Rincón Mountains, Pima County, Arizona. 2. Habitat of *Heloderma h. exasperatum* in tropical deciduous forest ("short-tree forest") near Alamos, Sierra de Alamos in background, in barranca region of southern Sonora, Mexico



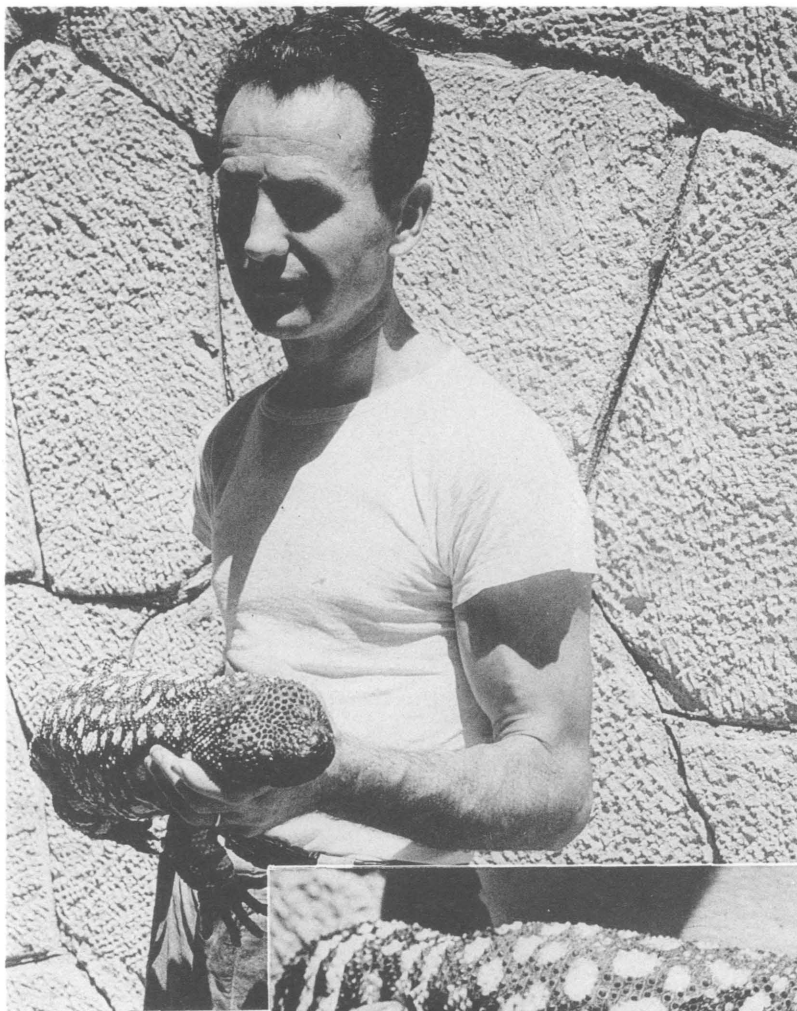
Adult *Heloderma s. suspectum* devouring half-grown hamster. Photographed in laboratory



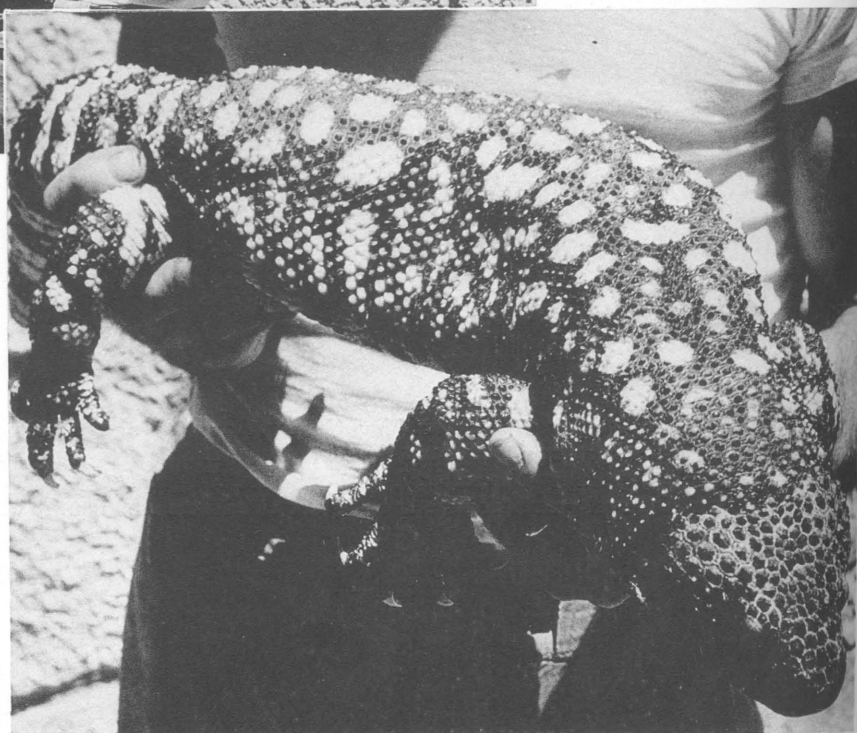
Adult *Heloderma s. suspectum* seizing and engulfing half-grown hamster. Photographs of successive stages cover an interval of approximately three minutes. Final photograph (8) shows downward flexure of head that invariably follows engulfment of mammalian prey



Adult *Heloderma s. suspectum* from Quijotoa, Pima County, Arizona. 1. Photographed April 25, 1951, when it weighed 347 grams, the approximate weight at time of capture. 2. On a diet of rodents, eggs, and horse meat, the same specimen 197 days later (November 8, 1951) weighed 656 grams, a 90 per cent increase in original weight. During same interval greatest diameter of tail increased from 21.0 mm. to 32.5 mm.



1

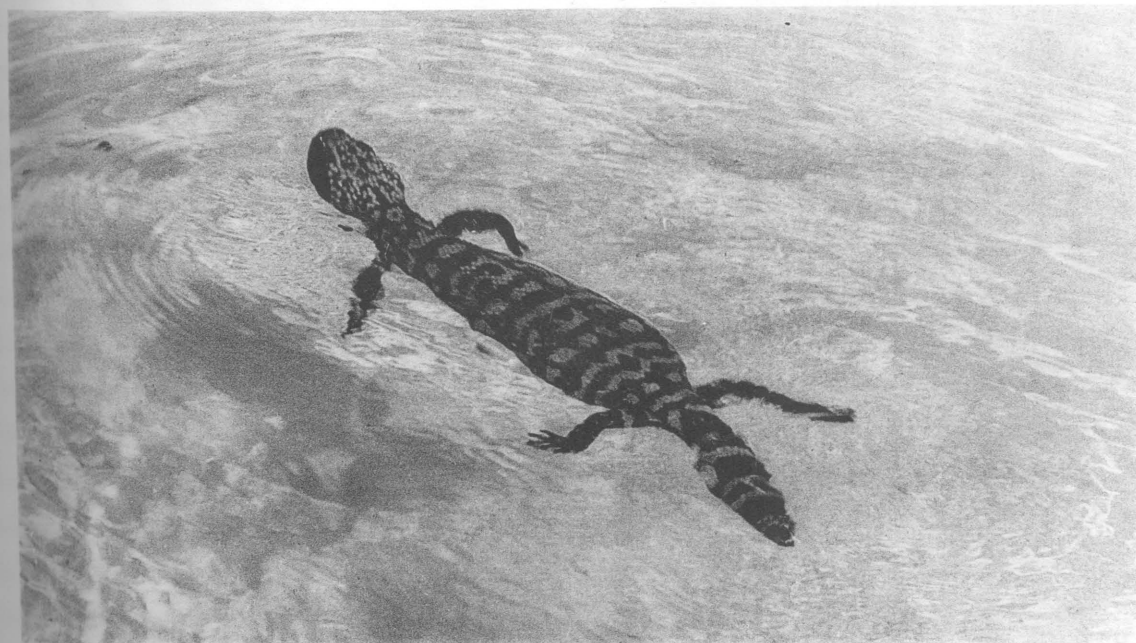


2

Adult *Heloderma h. horridum* of near maximum size in hands of Mr. John Werler, Curator of Reptiles, San Antonio Zoological Garden. Over-all length of lizard at time it was photographed, 780 mm.; weight, 4358 grams

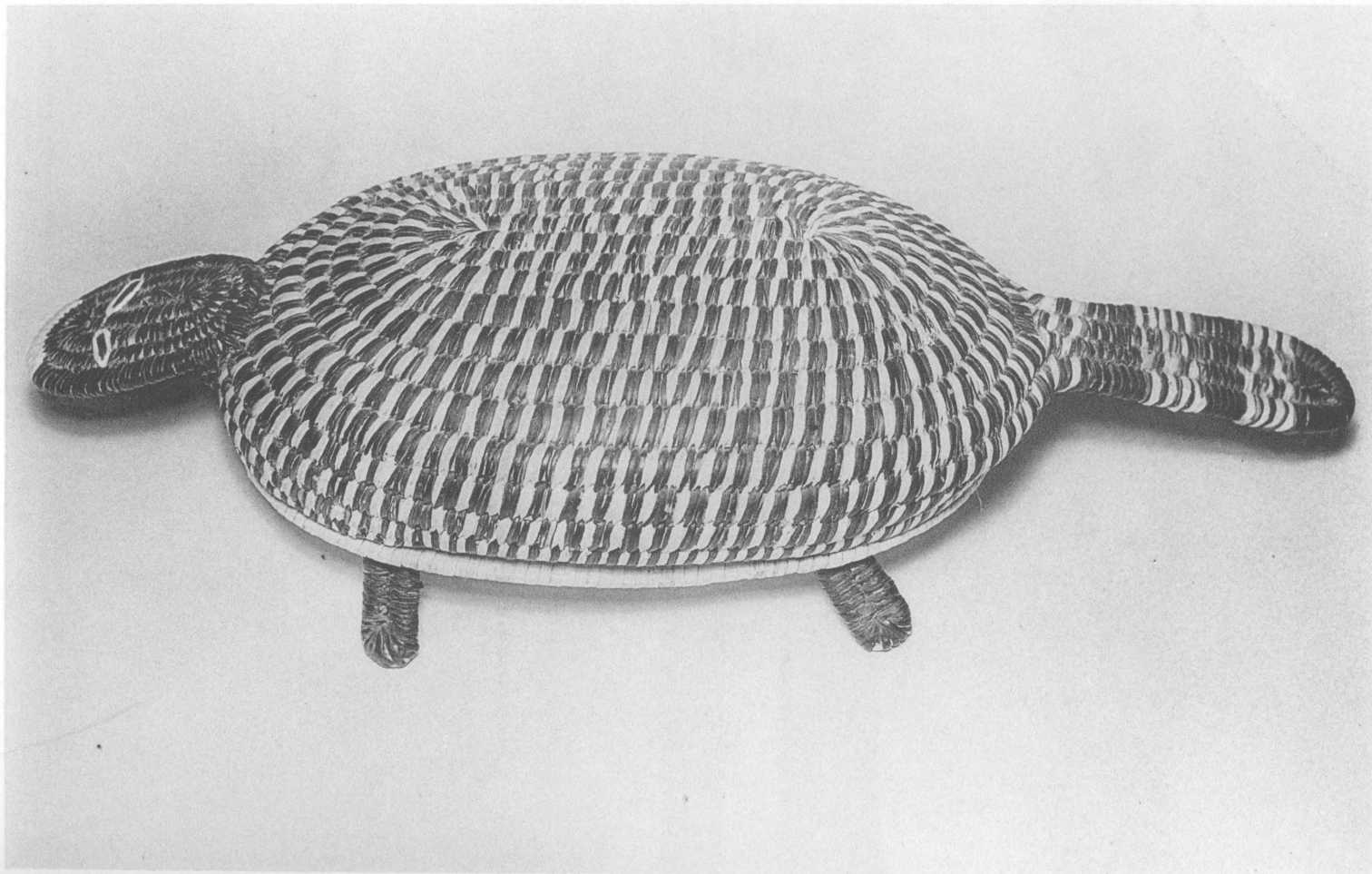


1



2

1. Eggs of *Heloderma s. suspectum* laid by captive specimen on July 29, 1952. Photographed following preservation. 2. Gila monster swimming. Photograph courtesy of Mr. George M. Bradt



Basket made by Papago Indians in Pima County, Arizona, intended to represent the Gila monster. Obtained by George M. Bradt in 1952. Photograph courtesy of Mr. George M. Bradt

sunlight at 2:20 P.M. on August 14, 1945. The experiment was carried out at the Boyce Thompson Arboretum on the edge of the desert 4 miles west of Superior, Arizona. At the beginning of the test the air temperature was 39.0° C. The surface temperature of the sand where the specimen was liberated was approximately 59° C., although a black-bulb thermometer placed on the ground had reached equilibrium at 71° C. at the time the test was started.

The lizard was allowed to crawl at its normal speed but was prevented from seeking shade. It was necessary to restrain it at three-minute intervals in order to obtain a record of its temperature. Three minutes after it was liberated, its cloacal temperature had risen to 34.9° C. (at 2:23); at 2:26 it had reached the level of 38.0° C. Three minutes later, at 2:29, the lizard was still crawling, with its cloacal temperature at 41.2° C. Within the next three minutes, approximately 11 minutes after having been exposed to the sun and the hot substratum, the lizard crawled with difficulty; symptoms of partial paralyzation began to appear; at 2:32 the cloacal temperature had risen to 42.5° C. The accelerated respiration doubtless dissipated some heat, but one minute later, 13 minutes after having been exposed to direct solar radiation, the cloacal temperature had reached 44.2° C., and the reptile was completely paralyzed.

At this juncture the lizard was removed from the sun and placed momentarily in cool water, where it revived in approximately five minutes when the cloacal temperature had dropped to 34.0° C. No sign of paralysis remained. A month later the lizard was still alive, and active. In some iguanids that have been tested the limbs often remain paralyzed after a lizard has reached the critical maximum. However, in the scincids and anguids that have been heated to this level, recovery is usually complete, as it seems to have been in the helodermatid.

Under natural conditions death would have ensued as a direct result of still higher body temperatures to which the lizard would have been exposed after it became paralyzed. It is improbable, of course, that Gila monsters are often forced to be abroad during the hotter part of a summer day. Brief exposures to body

temperatures slightly exceeding 40° C. can be tolerated, but as do other reptiles inhabiting arid regions, the Gila monster avoids long exposure to high temperatures by foraging at night and by seeking shelter below the surface when air and substratum temperatures reach higher levels than the maximum that can be tolerated. Contrary to Shufeldt's opinion (*supra cit.*), the Gila monster avoids prolonged exposure to direct solar radiation. Arrington's (*supra cit.*) statement that this reptile cannot endure the heat of the sun in summer is borne out by the one experiment conducted, and even if it be assumed that some variation would be encountered, the maximum temperature that a Gila monster can tolerate for even a brief period cannot greatly exceed 44° C. The critical maximum is doubtless reached at even lower levels by some individuals.

LOW-TEMPERATURE TOLERANCE

Towards the cooler end of the scale there are three levels in the body temperature of a reptile that are perhaps of more biological significance than others. (1) The first is the minimum temperature voluntarily tolerated. As noted above, a Gila monster was active at a body temperature of 24.2° C. Activities might be sustained at somewhat lower temperatures outside the laboratory. (2) The second is the critical minimum, defined by Cowles and Bogert (1944) as the temperature that causes a cold narcosis and effectually prevents locomotion. Another criterion has sometimes been used, namely, the ability of a reptile to right itself when turned upside down. This ability is commonly retained at lower thermal levels than those producing the narcotic state that inhibits locomotion. (3) Finally, the lethal minimum has been defined as the highest low temperature that will result in death after brief exposure.

The lethal temperature is the most difficult to define owing to the fact that resistance to freezing is affected by various factors, notably by the rate of cooling, the duration of the exposure, the water content of the animal, and the state of the contained water (that is, whether the water is a free solvent or bound by protein). The effects of rapid thawing are perhaps deleterious, and it is possible that less readily discernible physiological factors are of importance in determining the outcome of exposure

to subfreezing temperatures. A female lizard, for example, might be able to tolerate temperatures prior to ovulation that it could not tolerate with the onset of hormonal and other changes that accompany ovulation.

The necessity for considering temporal factors is a serious handicap in gaining a thorough understanding of the effects of low temperatures on reptiles. Variability in tolerance within the species requires the use of samples rather than individuals, and in the ideal experiment separate lots should be tested at various thermal levels for various periods of time. Furthermore it would be desirable to test groups of individuals taken at different times of the year.

This ideal has been far from achieved in our study of *Heloderma*. We have been able to test but three individuals, all adults from the vicinity of Tucson, Arizona. The tests were carried out during the winter when the lizards were inactive, although they had been maintained at room temperatures, which fluctuated between the approximate limits of 20° C. and 25° C. The first lizard tested was one weighing 420 grams. It was placed in a cold chamber where air temperatures were maintained within a degree of 5° C. Wet sand was provided on the floor of the container that held the Gila monster. When placed there at 11 A.M. the lizard had a cloacal temperature of 21.8° C. The temperature of the moist sand fluctuated

between 4.2° C. and 4.6° C. Fluctuations in the temperature of the lizard and their effects upon its muscular ability and coordination were recorded (see table 4).

At the conclusion of the 48-hour period the lizard was removed to a cage at room temperature, where it regained the ability to crawl within a half hour's time, when the body temperature reached a level of 14° C. No deleterious effects were noted as a result of the exposure. The lizard weighed 415 grams when removed, indicating a loss of but 5 grams during the 48-hour period. At the conclusion of the test the body temperature of the lizard was 0.6° C. higher than that of the moist sand of the substratum.

In a second experiment two Gila monsters were subjected to slightly higher temperatures for a 96-hour period. Whereas the two specimens were approximately equal in length (No. 1 was 305 mm. and No. 2 was 301 mm. from snout to vent), one was considerably thinner than the other; No. 1 weighed only 388.8 grams, while the heavier one, No. 2, weighed 492.8 grams at the beginning of the experiment. In this test dry sand was placed on the floor of the container inside the chamber. The sand varied in temperature from 7.5° C. to 8.6° C. during the experiment. Observations are summarized in table 5.

Although stimulated by being touched on the

TABLE 4
EFFECT OF LOW TEMPERATURES ON THE BEHAVIOR OF A GILA MONSTER

Date	Time	Cloacal Temperature in Degrees Centigrade	Behavior Noted
Feb. 17	11:00 A.M.	21.8°	Able to crawl, rights itself readily when turned on its back
Feb. 17	12:30 P.M.	8.5	Unable to crawl, rights itself with difficulty
Feb. 17	2:00 P.M.	6.3	No appreciable change
Feb. 17	4:00 P.M.	5.3	Barely able to regain normal posture
Feb. 18	9:00 A.M.	4.6	Extremely slow, but able to right itself, expels air from lungs when seized
Feb. 18	4:00 P.M.	4.6	Reaction identical with that at 9:00 A.M.
Feb. 19	9:00 A.M.	4.8	No change since previous day, reaction almost identical, but action in turning over is extremely slow
Feb. 19	11:00 A.M.	4.8	Still able to hiss when seized, and to turn right side up when placed on its back

TABLE 5
RESULTS OF PROLONGED EXPOSURE OF *Heloderma suspectum* TO LOW TEMPERATURES

Date	Time	Cloacal Temperatures in Degrees Centigrade		Behavior Noted when Seized or Prodded
		No. 1	No. 2	
Feb. 25	10:00 A.M.	26.8°	28.5°	Able to crawl but not active, tongue thrust out at irregular intervals
Feb. 25	11:00 A.M.	10.3	12.6	Barely able to crawl, tongue thrust out when lizard is seized
Feb. 25	12:00 M.	8.7	9.2	Unable to crawl, "tongue thrust" present, able to right themselves
Feb. 25	3:00 P.M.	7.7	7.7	Mouth opens slightly, but tongue no longer distended, loud hiss emitted when seized, able to right themselves, but unable to crawl
Feb. 25	4:00 P.M.	7.5	7.6	No appreciable change since 3:00 P.M.
Feb. 26	9:00 A.M.	7.5	7.2	No appreciable change since previous day
Feb. 26	11:00 A.M.	7.8	7.8	No appreciable change
Feb. 26	1:00 P.M.	7.4	7.4	No appreciable change
Mar. 1	10:00 A.M.	7.7	7.5	Hiss emitted when seized, No. 2 able to right itself; No. 1 cannot. Removed from chamber

back with the hand at intervals of one minute after removal from the chamber, neither lizard thrust out the tongue until No. 1 had regained a body temperature of 9.5° C. Both lizards were able to regain the prone position when turned on their backs within a minute after removal, although No. 1 was unable to do so when first removed. Feeble ability to crawl became manifest after 25 minutes' exposure to room temperature, No. 1 at 13.9° C. and No. 2 at 13.0° C.

At the conclusion of the experiment the body temperature of the lizards was from 0.8° C. to 1.0° C. lower than that of the dry sand upon which they had been resting. The slightly lower temperature of the lizard can be attributed to respiratory cooling, as this experiment was carried out in a relatively dry atmosphere. Each of the two lizards lost approximately the same amount of weight during the 96-hour period, 12.1 grams by No. 1, 12.0 grams by No. 2. When given access to a pan of water in the cage the original weight was regained within the next two days. Moisture loss is discussed in a subsequent section; here it need only be noted that on wet sand in a humid atmosphere in the first experiment the Gila monster's temperature tended to be a fraction of a degree higher than that of the substratum.

SUMMARY OF HEAT REQUIREMENTS

From the fragmentary evidence presented, the following tentative conclusions concerning *Heloderma s. suspectum* can be drawn:

1. The critical maximum or the upper limit of tolerance is reached at a level approximating 44° C., although variations in tolerance to high body temperatures may be anticipated. The mean lethal temperature is presumably slightly higher.

2. The upper limit of the body temperature voluntarily tolerated under laboratory conditions is 33.7° C.

3. The mean for the normal activity range is 28.7° C., with a marked "preference" for body temperatures between 29° C. and 30° C. The optimum for activity (but not necessarily for inactivity) falls between 28° C. and 31° C.

4. The voluntary minimum, or the lowest body temperature at which the lizards were foraging, digging, or carrying out routine activities, is 24.2° C., recorded for a captive assumed to be stimulated by hunger.

5. Below the minimum body temperature voluntarily tolerated the ability to crawl is still present until the approximate level of 10° C. is reached. The tongue can be thrust out at somewhat lower levels, but this response is

abolished between 8° C. and 9° C. At body temperatures as low as 4.6° C. the ability to hiss by the forcible expulsion of air from the lungs is still present, and even prolonged exposure (over 24 hours) to body temperatures near this level does not abolish this response nor the ability to regain the prone position when the lizard is turned on its back by artificial means. The critical minimum and the lethal minimum have not been ascertained.

6. Under natural conditions both *Heloderma suspectum* and *H. horridum* doubtless avoid exposure to extreme environmental temperatures by retreating beneath the surface. At the northern extremity of the range of the lizards

of the genus in southwestern Utah air temperatures slightly lower than -20° C. have been recorded, but *H. s. cinctum* doubtless seeks shelter in the fall before such temperatures are reached. Temperatures much below 20° C. are probably avoided by both species.

It has not been ascertained whether *H. horridum* is similar to *H. suspectum* in its tolerances to extreme body temperatures. However, it is noteworthy that the Mexican species is not known to occur in any region where air temperatures below freezing have been recorded. The northern limit of its distribution corresponds closely to the southernmost limit where frost occurs in Sonora.

MOISTURE REQUIREMENTS

Garman (1891) appears to have been the first to mention the Gila monster's moisture requirements. Garman notes that a captive "at once showed a fondness for lying in the water with his snout sticking out; this was varied by lying on the bank with his tail sticking in, a position which he apparently found to be very delightful." Whether a lizard's emotions include a feeling of delight may be questioned, but Garman's observation is sound. Duncan (1884) claims that captives "do not like water," and Sokolowsky (1912) asserts that helodermatids never willingly enter it. Wevers (1910) points out that this is a gratuitous assumption easily disproved by observation. A captive Gila monster that Wevers maintained often went into the water of its own volition. Fahr (1912) notes that a captive spent much of its time partly submerged, often with only the head resting on the edge of the container. Van Denburgh (1922) observes that the Gila monster "is very fond of water." Ortenburger and Ortenburger (1926) report that, "The cage in which they [16 Gila monsters] were kept was of good size with a flat water pan in one corner in the wet sand; under this pan were invariably found as many of the animals as could find a place, and most of the others were then in the water pan." Bogert and Oliver (1945) comment that "it is well known that captive specimens of each [species] prefer moist situations in cages, and often select pools of water," adding that "The aridity of the deserts to the west [of the range of

Heloderma] seemingly has prevented the genus from extending its range in this direction."

The latter interpretation requires some modification. It has seemed anomalous, not to say inexplicable, to many observers that a lizard inhabiting such arid regions as the deserts of Sonora, Arizona, Utah, and New Mexico should manifest a predilection for water. However, the Gila monster's apparent need for water in captivity is reflected in its habits, behavior, and distribution under natural conditions. Helodermatids obtain water from their food, mostly from that present in the tissue of their prey or from the eggs consumed. It is doubtful whether oxidative water (see Fat Storage above) plays a very important role in filling their needs for water, which is available as such during much of their season of activity, even in the deserts inhabited by *H. suspectum*. Like other reptiles helodermatids conserve water by excreting concentrated or crystalline nitrogenous waste. Actual tests have not been made, but it may be assumed that some, but relatively little, moisture is lost through the skin. Some is certainly lost through the surfaces of the lungs; the amount would depend upon the rate of respiration, the temperature, and the relative humidity of the inspired air.

Conservation of water in ectothermic animals can be achieved: (1) by estivating during the dry season; (2) by restricting surface activities as far as possible to the hours of darkness when temperatures are lower and relative hu-

midities tend to be higher, or by venturing out during the daytime largely during or after rains; (3) by seeking seclusion in burrows during daylight hours or while estivating. These are precisely the things that helodermatids do. It should be borne in mind that even in desert regions the relative humidity in burrows remains at a high level (Vorhies, 1945) even during the dry season. Moreover, a helodermatid can maintain its body at relatively low thermal levels, with respiration reduced accordingly, while the lizard is quiescent in a sanctum of the sort. When maintained in a cage where a burrow cannot be constructed, therefore, a helodermatid seeks any source of moisture provided, wet sand if available, or a water container if there is no alternative.

As discussed elsewhere in this report, the distribution of *Heloderma suspectum* reflects its need for surface moisture during the period of the year that it is active. While the increased aridity beyond the western extremity of the range of *Heloderma suspectum* may be a factor inhibiting the western dispersal of the animal, as Bogert and Oliver (*supra cit.*) suggest, it is probably of greater significance that west of the Colorado River in California, winter is the season of maximum precipitation, with relatively little during the summer months. Throughout the range of *H. suspectum* the summer months are not only sufficiently warm to permit the Gila monster to venture to the surface, but also sufficiently moist to supply the lizard's water requirements. It is not without significance that the western periphery of the range of the Gila monster corresponds closely to the line indicating the 2-inch average for warm-season (April to September) precipitation, as mapped by the United States Department of Agriculture (1941, p. 712). The western periphery of the saguaro, the giant cactus characteristic of much of the territory inhabited by the Gila monster, is almost co-extensive with that of the lizard, and seemingly reflects the need of the cactus for moisture during the warm season.

While the lack of summer rain explains the failure of *Heloderma* to penetrate California (where it may yet be found in a small area south of the southern tip of Nevada), it does not explain its limited penetration of Utah and southern New Mexico. At the north,

thermal factors or the shorter summer may supply an explanation, but it is far from obvious why Gila monsters have such a limited distribution towards the east. These lizards occur farther eastward than the saguaro cactus, but it remains uncertain whether the range of the Gila monster actually extends across the continental divide in southern New Mexico, as the sight records reported by Koster (1951) inconclusively indicate. Two specimens have now been obtained at Silver City, which lies immediately east of the divide at an elevation of 5931 feet. The habitat is atypical for the Gila monster, which does occur in the Upper Sonoran Zone in Arizona but not in the juniper-piñon association that surrounds Silver City. It is possible that both specimens reached this outpost as the result of human transport.

All authenticated records for southwestern New Mexico are on the Pacific drainage. Gila monsters are scarce in the Peloncillo Mountains not far west of the divide, but none has been seen in the Big Hatchet Mountains not far to the east. A geologist, Mr. Robert Zeller, has been working in these mountains almost constantly for well over two years. Several species of reptiles have been secured for the American Museum by Mr. Zeller, but thus far he has not seen *Heloderma*. The habitat appears to be as suitable as the localities in the Peloncillo Mountains where it has been taken. It is perhaps noteworthy that *Coleonyx variegatus*, a gekkonid lizard somewhat more nocturnal than *Heloderma*, has a similar local distribution. We obtained specimens in Granite Pass in the Peloncillos, but failed to find any farther east, despite a diligent search. The hiatus in the range of the genus, with another species (*brevis*) farther east as mapped by Klauber (1954a), seems to be real and not merely the result of inadequate efforts on the part of collectors.

There is, therefore, no ready explanation for the failure of *Heloderma suspectum* to extend its range farther eastward into southern New Mexico. The continental divide in this region is too low to present any physiographic barrier, for the Gila monster occurs at higher elevations in the Peloncillo Mountains. Presumably, therefore, the answer must be sought among the ecological factors affecting the distribution not only of the Gila monster but of other lizards as well, for two species of *Sceloporus* (*poin-*

setti and *jarrovi*), which live side by side to the south in Chihuahua, remain on opposite sides of the continental divide north of the international border.

At the south *Heloderma suspectum* is replaced by *H. horridum*, with an area between the ranges of the two species where no specimens of the genus have yet been taken. The southern periphery of the range of *H. suspectum*, however, is nearly co-extensive with that of the Sonoran Desert (Shreve, 1942). South of Guaymas, Sonora, there is a rather abrupt change in the flora, with numerous tropical elements present that are perhaps restricted to regions where temperatures never drop below freezing. The ranges of several species, both plants and animals, characteristic of the desert do extend farther south, not a few of them reaching northern Sinaloa, where *H. suspectum* may yet be found. Similarly, a number of tropical elements extend into southern Sonora, where there is an interdigitation of tropical and desert elements, as pointed out by Bogert and Oliver (1945). However, the two species of *Heloderma* differ so little in their food and feeding habits that there is no likelihood of their surviving together in the same areas.

Too little is known concerning the ecological

requirements of *Heloderma horridum* to attempt to account for the distribution of the species. Like *suspectum*, it is largely restricted to areas of xerophytic vegetation, even though it occurs in adjacent habitats, with its range extending well into the foothills of the Mexican Plateau where suitable conditions obtain. Its existence on the Atlantic slope, however, is restricted to the subhumid corridor of Chiapas, as noted in the description of the habitat of *H. h. alvarezi*. Despite the inclination of the *escorpión* to seek out water when in the laboratory cage, there is evidently an avoidance of humid regions.

While the aquaphilic (but not aquatic) behavior of the Gila monster and its congener are explainable in terms of moisture conservation, we cannot as yet explain the lizards' restriction to habitats that are largely xerophytic. Thermal factors cannot be eliminated, but it seems more probable that an explanation may be found in some phase of their reproduction, or in their feeding habits. Whatever the explanation, it is plain that helodermatids are rather narrowly adapted to their particular mode of existence in moderately arid regions as well as in deserts, even though truly barren regions are avoided.

ENEMIES

Jackson (1941) asserts that man is about the only creature that the Gila monster has to fear. There can be no doubt that human beings have become one of the more important, if not the principal, enemy of helodermatids. Still, it is difficult to believe that, aside from man and parasites, these lizards have no natural enemies among possible reptilian, avian, or mammalian predators. Except for the dubious account of a combat between a Gila monster and a snake (Anonymous, 1879), we are unaware of any reports of attacks except those by dogs.

Hensley (1949) quite incidentally mentions a Gila monster attacked by a dog. Reports cited below indicate that dogs are occasionally bitten while attacking the lizard. Other dogs display sufficient caution to avoid the lizard's teeth, however. Mauldin (1949) describes an encounter, doubtless relying on his memory and making assumptions that are more literary than scientific. He states that "like rattlers, Gilas

can't stand the desert sun, and every time this one would break out of his shady bush and start for his hole, the dog would let him get a little way out into the sun, then bedevil and confuse him and force him back into the bush, all the while barking and yapping to attract us to the scene."

Coyotes (*Canis latrans*) may attack Gila monsters, or they may avoid them. Dr. Charles Lowe of the University of Arizona tells us that he observed a badger (*Taxidea taxus*) eject an adult Gila monster from, presumably, the badger's burrow. The badger did not attack the lizard, however, and it was assumed that the lizard had inadvertently sought cover in the occupied burrow, to the mammal's distaste. Whether any raptorial birds are capable of subduing helodermatids is problematical, but juveniles may fall prey to hawks or owls. Some of the larger hawks do not hesitate to attack rattlesnakes, which are, of course, equipped with a

more efficient means of injecting venom than helodermatids. Snakes inhabiting the same territory as the Gila monster or the *escorpión* prey on other lizards, but thus far there is no evidence that even juvenile helodermatids are ever eaten by such reptiles. The account of Anonymous (1879), mentioned above, includes the statement that "The first Gila monster Mr. Parker ever saw was on the Salt River, ten miles from Phoenix. It was about 14 inches long, and was in combat with a snake four feet in length. The snake coiled in the usual manner, and as the monster advanced struck his blow firmly, producing no effect on the tough scaled

skin of his foe. The monster then rushed the snake, and seizing it with its arms and legs gave two or three bites, then let the snake go. The latter crawled away slowly, seeming to be badly hurt. The monster also took refuge in the brush." This may or may not be a reliable account, but we are not inclined to accept it, because most of the other information supplied to Anonymous by Mr. Parker belongs in the section dealing with folklore. Haddon (1954) obviously forced a Gila monster to bite a red racer (*Masticophis*) in order to obtain photographs.

REACTIONS TO ENEMIES

Gila monsters react to the presence of other vertebrates in divers ways. On being placed in a large cage (fig. 32) with several smaller iguanid lizards, as well as toads (*Bufo*), a Gila monster displayed no reaction to their presence, until it approached a large toad, *Bufo alvarius*, a species that occupies much the same range as *H. s. suspectum*. The lizard made exploratory movements, thrusting out its tongue repeatedly as it did so. As the tips of its tongue either came close to or actually touched the toad, the lizard paused and then slowly retreated, crawling backward for a few inches before turning aside. Toxic as well as irritating substances produced by glands in the skin of the toad may account for the reaction in this instance.

Later a rattlesnake, *Crotalus atrox*, a species that also shares much of the range of the Gila monster, was introduced into the same cage. The lizard in the course of its explorations eventually approached the rattlesnake, which held its ground coiled in the position assumed when it is ready to strike. This time the Gila monster did not come closer than approximately half a meter before it seemingly became aware of the snake. At this juncture it promptly turned completely around and fled with more than its usual speed. However, Gila monsters that had been in captivity for several months did not react in the same fashion and seemed oblivious to the snake's presence. Ditmars (1907) writes that Gila monsters caged with harmless snakes "are crawled upon amid a display of good nature on either side."

Woodbury (1928) reports that "some of the different kinds of snakes and lizards [living in southwestern Utah] will live amicably together in confinement, but not so the Gila monster—on two different occasions when I put a rattlesnake in with a monster, the snake was killed. Teeth marks in the snake showed plainly how it had been done." Woodbury does not say how closely confined the lizards were. Arrington (1930) describes similar incidents in greater detail but likewise fails to state whether the cage was large or small. His observations were made in Arizona.

According to Arrington when a Gila monster is "placed in a cage with a rattler [it] shows no fear, and seems to recognize its superiority, while the snake, from the first, considers the monster a foe, and usually glides to the farthest corner of the cage. The lizard follows menacingly, and slowly moves up to the rattler until in a striking position [?]. Then with a quick swing it imprisons the rattler's body in its jaws and characteristically hangs on. The snake thrashes about, but seldom attempts to strike its deadly opponent. If a strike is made, no effect is apparent, and the fangs do not seem to penetrate the thick armored skin of the lizard. Three to five minutes are sufficient to quiet the average rattler and bring death, and then only does the victor loosen its grip on the snake's body. If the lizard battles an unusually large rattler, four and a half feet or over, death may not result, but for days the snake will appear very sick and almost lifeless."

This account is of interest because it provides

some notion of the protective utility of the Gila monster's osteoderms. It will be noted, however, that the observations reported by Woodbury and by Arrington are not in agreement with ours, for in our test the Gila monster fled from the rattlesnake when the two were together in a large cage. We suspect that different results might have been obtained in our laboratory had we confined the rattlesnake and the Gila monster to a restricted area. When in close quarters, with no opportunity to retreat, such fights as those described by Arrington may well occur. However, when either the rattlesnake or Gila monster is able to avoid the other it seems probable that it does so.

When confronted by a mammalian enemy the Gila monster ordinarily flees, taking refuge in a burrow if one is accessible. If intercepted the lizard will defend itself, employing its jaws if an opportunity is afforded and its aggressive posture and behavior fail to discourage the attacker. Ortenburger and Ortenburger (1926) mention the aggressive behavior of a Gila monster at the time of its capture: "It does display surprising speed and dexterity in lateral movements of the head and the bending of the body in the same direction. In one case when an attempt was made to hold a Gila monster down with the barrel of a pistol, the animal snapped and bit the barrel with such force as to break several of its teeth. Even this did not cause the animal to relinquish its hold." As Zim and Smith (1953) phrase it, "Gila monsters can twist their heads, bite swiftly and hang on strongly."

Arrington (1930), with anthropomorphic overtones, describes the reactions of a Gila monster encountered in the field. The lizard, easily overtaken in open terrain, "soon realizes that its rush for liberty is fruitless, and again it stops, apparently in complete submission. However, such is not the case, for an attempt to pick it up will prove disastrous. The immovable attitude is held until our hand is twelve inches or less from the side of the reptile's head. Then with a sudden hiss and wide open jaws it strikes to the side, pivoting on its rear legs." Arrington provides an even more exaggerated impression of the lizard's speed, however, when he continues, "the eye cannot follow the lightning action, and anything within range of those powerful jaws is quickly imprisoned

in their bull dog grip. An agile individual may completely face about in its enraged strike, accurately grasping anything less than five inches from the ground."

These two accounts describe the behavior of Gila monsters under exceptional conditions; more commonly it is not so difficult to capture these lizards. A Gila monster held down and grasped by the neck may display no reaction beyond emitting a hiss. An adult *escorpión* taken in southern Sinaloa was not particularly aggressive when it was intercepted, and made no great effort to bite when it was picked up in the hands. Human enemies may not evoke the same reaction as other mammals when they approach a helodermatid. Hensley (1949) mentions that a Gila monster disgorged a nestling cottontail when attacked by a dog. Such reactions sometimes accompany the emotion of fear in higher animals; the basis for the reaction in the lizard may be similar.

Not all dogs manifest sufficient caution to avoid being bitten. Mr. William Woodin, 3rd, has supplied us with an account of a high school student who was bitten by a Gila monster after capturing it and placing it in a sack. The student includes the information that his dog got to the animal first when it was discovered on the road. The dog was bitten on the "face," with no ill effects beyond "vomiting that night." Jackson (1941) mentions a small dog's having its foreleg broken by the bite of a Gila monster.

Another account of a dog's encounter is quoted by Anonymous (1890a) from an article said to have been written by John A. Spring. The story relates that "Near Magdalena, Sonora, a man was hunting rabbits with a dog. The latter inserted its snout into a rabbit hole, but immediately retreated, uttering fearful howls while he was trying to shake off a Gila Monster, which had fastened its teeth in the dog's nose, and although snarling and spitting without interruption, could not be made to let go its hold till it was killed, and even then its jaws had to be forced apart with an iron rod. The dog soon began to act strangely, and showed something like the same symptoms a horse does when suffering from the 'blind staggers,' but soon began turning around itself around in a circle, and in about 20 minutes fell down dead. The same actions before death were

observed in a mule, only this animal was bitten in a hind leg, and lived for several days."

The story seems at least plausible, although the gullibility of Spring is reflected in other yarns included in his account. There is no indication that Spring witnessed the encounter, which may have been embellished by his informant or by the author himself. It can

scarcely be doubted that helodermatids have occasion to defend themselves from other predators, but if any encounter of the sort has been observed we are unaware of its being reported. Bradford (1895) mentions that a Gila monster bit a dog on the lower jaw, and the dog "had to be choked."

ADAPTIVE COLORATION

The pattern and coloration of the various subspecies of *Heloderma* are depicted as well as described in some detail in the taxonomic account and in the section dealing with clines. As noted therein, there are ontogenetic changes as well as geographic trends, aside from a fair amount of variation in the pattern and coloration of the adults representing any local population. The dorsal markings of adults range from the more or less banded pattern of the juvenile that is retained in the adult of *H. suspectum cinctum* in Utah at the northern periphery of the range to the nearly uniform slaty black of *H. horridum alvarezi*, with the merest vestiges of a pattern in Chiapas, at the southern extremity of the range. The coloration varies from black and yellow, more characteristic of *cinctum*, to black or blackish brown and yellow, through various shades of pink to moderately reddish in *H. s. suspectum*. *Heloderma h. exasperatum* more closely resembles *suspectum* in color but has a pattern closer to that of *H. h. horridum*. The latter is extremely variable in coloration, with the lighter elements of the pattern varying from lemon yellow to red, while the darker reticulum ranges in color from black to brown. The southernmost population, *H. h. alvarezi*, inhabiting what appears to be the most generally humid region occupied by lizards of the family, is almost uniformly black, with a few lighter areas appearing as dots or spots, or representing vestiges of the lighter bands on the upper surface of the tail; in preserved material the lighter areas are whitish, but they may have been yellowish in life.

The coloration of helodermatids, as noted in the section dealing with clines, conforms to the principle of Gloger's rule, with the darker populations inhabiting the damper regions, and the palest coloration present on individuals

from populations living in the more arid portions of the range of the genus. Gadow (1901) and H. W. Parker (1944), among others, have referred to the "warning coloration." Cott (1940), unaware of the north-south trend in color, interprets the pink and black or black and yellow coloration as aposematic coloration. He writes, "In the case of lizards, the majority of desert-dwelling species depend for safety upon cryptic appearance, alertness, swiftness of foot, and burrowing habits; but in contrast to such forms, *Heloderma suspectum* and *H. horridum* [which inhabits xerophytic areas, but is not a desert-dweller] stand out as striking exceptions. These ugly brutes, coloured respectively pink and black, and black and yellow, are notorious as the only poisonous members of the whole group; and correlated with the aposematic appearance and poisonous properties we find them as ill-equipped for speed as they are defiant and formidable."

Cott's argument was more convincing prior to the discovery of the slaty-black race of *H. horridum* inhabiting Chiapas. If aposematic coloration is of much adaptive value, it would be difficult to explain its absence in the Chiapas population. It may not be fortuitous that the reddish or pinkish coloration is more widely distributed in populations near the center of the range of the genus, and Cott does, of course, cite other venomous reptiles that provide evidence to bolster his arguments. Nevertheless, there are innumerable reptiles that are both slow and venomous and that do not have colorations that can by any stretch of the imagination be interpreted as aposematic.

Of more importance, perhaps, the pattern and coloration of helodermatids are more readily interpreted as being cryptic in nature. Cott (*op. cit.*) himself notes that "many highly

colored animals are actually cryptic in nature: indeed, we are faced with the paradox that in certain cases the most effective self-effacement in the field will demand a costume which in the museum will present a most effective self-advertisement." Anyone who has collected Gila monsters at night in their native habitat must have been impressed with the cryptic value of their markings. When seen on the unnatural background of a paved road the lizard is conspicuous. But as it hastens its gait to avoid the approaching collector, the lizard usually manages to crawl off the edge of the black surface of the road. Thereupon it appears to vanish, its body merging into the background of rocks, or vegetable debris that commonly litter the surface of the ground. Unless the movements of the animal can be followed as it leaves the road, it is extremely difficult to locate the Gila monster, particularly if it comes to rest at the base of a shrub. The sharply contrasting bands or the reticulum of light and dark admirably serve to disrupt the body outline under such conditions. Far from being conspicuous, the pinkish or yellowish coloration blends with the background, which in desert regions often contains moderate amounts of red pigment. Or the pink feldspars of granitic rocks, so often present in the habitats of *H. suspectum*, may serve to enhance the resemblance of the lizard's lighter colors, with the shadows from the irregular rocky surface being matched to some extent by the dark reticulum of the lizard's pattern.

The basically similar pattern of *H. h. horridum* must be equally effective under such conditions. The regions inhabited by this subspecies are more densely covered with vegetation than the deserts (or "desert steppe" in some classifications) inhabited by *suspectum*. We have no precise information concerning the habitat of *H. h. alvarezi*, beyond knowing that it has been found thus far only in localities restricted to the subhumid corridor of Chiapas as delineated by Stuart (1954). We do not know whether the black beaded lizard, or *escorpión negro*, lives in areas where the vegetation is sufficiently dense to shade the substratum almost completely, but it is manifest that the extremely dark coloration of the lizards of this race would be advantageous under such conditions.

In any discussion of their coloration it should be recalled that helodermatids are largely nocturnal. To the human eye at least the gaudy coloration is not conspicuous when seen in the moonlight, even on clear nights in the desert when the moon is full. Whether the gaudy colors are more readily apparent to other predators than they are to human beings under such conditions is perhaps a matter of conjecture. Birds are not color blind, but mammals other than primates probably are (Maier and Schneirla, 1935), if we may judge by the tests that have been made of a few species. Some reptiles are evidently able to discriminate between colors, but the information currently available is too fragmentary for any reliable generalization to be made.

While it is difficult to assess the validity of Cott's conclusions, it is pertinent to note that the combination of color and pattern may serve a dual purpose. The pattern renders the animal inconspicuous in its normal habitat, perhaps more so at night than during the day. But when seen in the open in daylight the coloration of helodermatids other than *alvarezi* may indeed provide "effective self-advertisement." Any enemy that had previously suffered from the effects of the lizard's venom might well avoid an encounter with a second individual. Still, it seems questionable whether the presence of reds, pinks, or yellows would materially affect the behavior of predators, or serve as a deterrent to attack. If helodermatids are indeed "identified" by potential predators as animals to be avoided, it is probable that sensory cues other than, or in addition to, color discrimination are employed.

To us it seems more reasonable to consider helodermatids adapted primarily for concealment in their natural habitat at the time when they are most often active, namely, at night. Those abroad during the day or that venture to cross roads or other open, more or less smooth terrain are the animals most readily seen by collectors, who may, indeed, think of helodermatids as being far from cryptic in their markings. But there is no way of ascertaining how many Gila monsters or *escorpiones* are overlooked in the field. The cryptic nature of the lizard's pattern becomes impressive only after the collector has seen the lizard first on the uniform pavement of a highway at night,

and then has been confronted with the problem of locating the lizard either in the moonlight or in the beam of his light, as the animal crawls off into the rocky terrain adjoining the road.

It is noteworthy too that the only other lizard commonly abroad at night in the area occupied by the Gila monster is the banded gecko (*Coleonyx variegatus*), a lizard with a pattern that is basically similar to that of the

helodermatid. The much smaller gecko is marked with dark cross bands or sometimes with a mottled coloration on a pinkish or flesh-colored ground color. By virtue of its size it is, of course, much less conspicuous than the Gila monster, but it is readily seen on paved roads, and considerably more difficult to see when it escapes to the natural terrain bordering a highway.

DEFENSE

From the preceding discussions it may be seen that helodermatids avoid enemies passively, actively, or even aggressively. Other means of avoiding enemies require no discussion. The adaptive modifications discernible in helodermatids involve specializations in morphology and behavior that we shall attempt to summarize. Passively the lizards are protected as a result of their habits or attributes by:

1. Remaining in seclusion or avoiding exposure when not actively hunting. Inactive helodermatids seek the security provided by underground retreats. These may be the burrows of mammals or they may be dug by the lizards themselves. Fat storage, discussed elsewhere, is primarily an adaptation to an environment subject to drought but may be mentioned in this connection as a specialization that permits the lizard to avoid exposing itself to predators for prolonged periods.

2. Their cryptic coloration. When on the surface in their native habitats, particularly during their period of greatest activity at night, helodermatids escape detection as the result of their pattern and markings. These tend to obscure the outline of the body; the darker elements of the various patterns characteristic of local populations blend with the shadows cast by the rocks or vegetation in their native habitats, while the lighter elements harmonize to some extent with the highlighted portions of the substratum. In the open terrain devoid of vegetation, the pattern and coloration may cause the individual to be conspicuous, but it is doubtful whether the red, pinkish, or yellow pigments often present are of any great importance as "warning coloration."

3. Their armor. The osteoderms embedded in the thick skin provide a measure of protection from the teeth and perhaps even from the

fangs of predators.

Actively helodermatids protect themselves by:

1. Retreating. While not rapid in their movements, the Gila monster, and probably the *escorpión* as well, sometimes manage to escape a pursuer by the simple expedient of flight, seeking refuge in any burrow that is available. Sometimes Gila monsters behave as though they knew the precise location of the burrow into which they flee. Whether this is indicative of familiarity with the surrounding terrain or the repeated use of a single burrow has not been established.

2. Intimidating an attacker. Helodermatids hiss, audibly expelling the air from the lungs, and sometimes open the mouth. If the enemy approaches, the lizard may lunge in its direction. Such gestures serve to intimidate such mammals as dogs, and may well discourage the attacks of other possible predators.

3. Biting. If other means of discouraging enemies fail, and a predator comes sufficiently close or actually seizes a helodermatid, the grooved teeth are brought into play. As innumerable authors have noted, an angry helodermatid retains its grasp with remarkable tenacity, holding on sometimes for as long as 15 minutes. The venom apparatus is sufficiently formidable to protect the lizard from the majority of its potential enemies.

The venom apparatus of snakes, while used secondarily as a means of defense, seems to have evolved primarily as a means of killing or subduing their prey. The cruder venom apparatus of *Heloderma* certainly plays no important role as far as its food-getting activities are concerned. It unquestionably is of survival value as a protective device. Shufeldt (1887) states that "Professor Cope seems to think that

this lizard has slowly developed its venomous apparatus from being sluggish in its movements, and consequently ill adapted to get out of the way of larger animals and not be trodden upon; this constant source of irritation and danger has in the long ages gradually rendered its saliva poisonous and eventually given rise to the development of a special gland and apparatus for the purpose."

Natural selection, as implied by but not explicit in, Cope's statement, offers the simplest explanation for evolution of the specialized saliva and the concomitant acquisition of

grooves in the teeth. Our knowledge of the origin and history of the group is too limited to enable us to provide any estimate of the length of time required for the evolution of the relatively crude venom apparatus. The teeth, however, appear to have changed little if at all since the Oligocene (Gilmore, 1928). It may be inferred that the venom apparatus has been one of the more important factors in the survival of these primitive varanoids (or platynotids) during a period of at least 40 million years and probably longer.

PARASITES

As compared with other lizards, helodermatids appear to be remarkably free of nematodes, tapeworms, linguatulids, or the other larger internal parasites so commonly observed in the coelomic cavity of reptiles. In more than a hundred viscera that were examined, parasites were noted in only two. One *H. s. suspectum* from near Tucson, Arizona, contained an encysted parasite identified by Dr. Libbie H. Hyman as an acanthocephalid worm, and a second specimen from the same region contained an unidentified tapeworm. Ryerson (1949) reports that two out of seven Gila monsters from the vicinity of Tucson contained microfilariae, in one of which the adult worms were taken from the heart and aorta. Hemogregarines were present in the same animal. Ectoparasites were encountered on only one individual from the field, a specimen of *H. h. horridum* from Tehuantepec, México, that had a tick attached to its abdomen. While in captivity some Gila monsters became infected with mites of the same species that infested snakes kept in the same laboratory.

Woodson (1949a) quotes informants who state that these lizards have also "died from having lice, as well as from pneumonia," but offers nothing to indicate that the statement is based on reliable evidence. Helodermatids may well be afflicted with mites, especially when kept in zoological gardens where precautions must

be taken to avoid the spread of infestations. Woodson also mentions "canker of the mouth," but no effort had been made to identify the causative organism.

There are undoubtedly many more parasites present in helodermatids than our inexperienced search disclosed. Nevertheless, anyone who has examined the viscera of any number of agamids, iguanids, or geckos is certain to have been impressed by the general prevalence of nematodes and tapeworms, in particular, in such lizards. The absence of such conspicuous parasites in helodermatids is striking. We are tempted to suggest that the nature of their diet may be a factor involved in their avoidance of parasites so commonly found in other lizards. Parasites or their ova must infrequently be ingested with the avian eggs that comprise a major portion of the food consumed by *Heloderma*, and perhaps even the fledgling birds or the nestling mammals that are also important in their diet are less heavily parasitized than adult animals of the same species. In other words, the nature of the lizards' diet would seem to reduce the probability of their ingesting so many parasites as would be the case did they habitually prey upon adult animals. As carrion is eaten infrequently, there is relatively little opportunity for these lizards to ingest the parasites transmitted by older animals.

VENOM APPARATUS AND THE VENOM AND ITS EFFECTS

HISTORICAL RÉSUMÉ

EARLY DESCRIPTIONS

THE ESCORPIÓN (*Heloderma horridum*) probably acquired a sinister reputation shortly after the Spaniards made their acquaintance with it. Long before the end of the colonial period Francisco Hernández, in a manuscript completed in 1577 (von Hagen, 1944), had described the lizard and mentioned its evil reputation. His account, in an extract from his works annotated and translated by Father Francisco Ximénez, was published in México in 1615. In the quaint Spanish of the period, retained in an 1888 edition reprinted under the direction of Nicolás León, Hernández writes: "*La mordedura deste animal aunque es dañosa no es mortal, por lo qual se tiene por mas horrible á la vista, que no en la herida, y nunca suele hazer mal anadie si primero no es ofendido, y prouocado.*" [The bite of this animal, though harmful is not mortal, for which reason it is more dreaded for its appearance than for its bite, and it never tends to harm anyone unless offended or provoked.] After more than three hundred years this is a fair statement, the more impressive for having greater validity than many comments regarding *Heloderma* published within recent years.

Whether the early Spanish settlers in México discovered that *Heloderma horridum* was venomous or obtained their information from Indians resident in the region, the name "*escorpión*" was already employed by the Spaniards inhabiting Cuernavaca at the time Hernández wrote. In Spain the name "*escorpión*" is used to designate the same sort of arthropod that in English is called a scorpion (Latin *scorpio*, Greek *skorpios*), a creature equipped with a poisonous sting at the posterior end of its body. In ancient times the name, with implications that seem obvious, was also applied to a scourge armed with metal points. Similarly the term has been used for various animals; such names as "scorpion fish," "sea scorpion," "water scorpion," or "scorpion fly" presumably having been coined in allusion to the presence of spines or a sting. As an extension of the original meaning, the name "scorpion" has also been applied to animals supposed to be, or suspected of being,

dangerous. In portions of the United States, notably Florida, adult skinks of the genus *Eumeces*, particularly those with conspicuous red heads and believed (erroneously) to be venomous, are called "scorpions." It is uncertain, however, whether this name was independently applied by English settlers in Florida, or, as seems equally probable, the usage can be traced to the Spanish inhabitants of an earlier era. Nevertheless at an early date the word "scorpion" had divers applications in the English language, having been applied to a reptile by the Reverend Charles Owen (1742) in his "Essay" published in London. Owen writes of "The Scorpion-Lizard" as follows: "'tis commonly called so, but is no more like it than a Hedge-Hog . . . quick in its Motion on the Ground, and very nimble in running up Trees; has several Rows of Teeth, and is reckoned to be of a very poisonous Nature."

Similarly the use of the name "*escorpión*" for *Heloderma* in México undoubtedly carried with it the connotation that the animal was endowed with evil attributes. This is further reflected in other beliefs (discussed under the topic Folklore) concerning the animal that Hernández mentions. It is not clear from his account, however, whether these notions were entertained by the Spanish settlers or by the Indians, both of whom must have been well aware of the potentially dangerous bite that could be inflicted by the lizard.

Wiegmann (1829) was acquainted with Hernández' earlier description, from which he quotes. Wiegmann also observed the grooved teeth in the type specimen, comparing them with the grooved fangs of such opisthoglyphs as *Homalopsis* and *Dipsas*. Within the next few years several authors (Wagler, 1830a; Schinz and Brodtmann, 1833; Wiegmann, 1834; and Duméril, Bibron, and Duméril, 1836, whose plate was copied from that of Wiegmann) depicted the type specimen in color and commented on the grooved teeth and the venomous nature of the species. Gray (1845) mentions the grooved teeth, and in 1857 writes, "this lizard is said to be noxious." Richard Owen [1845 (1840-1845)] observes that the

teeth are "sharp-pointed, with a deep fissure." Troschel (1853) not only describes the teeth in some detail but depicts the skull and other features of the anatomy and quotes Wiegmann's (1829) suspicions with reference to the function of the grooved teeth.

Kaup (1865) reviewed previous work and added a few remarks based on a juvenile example. Gervais (1873a, 1873b) depicted the skull in more and better detail than his predecessors, and was the first to include figures of cross sections of the grooved teeth, along with lateral views showing the groove. Duméril, Bocourt, and Mocquard [1878 (1870-1909)] illustrate the dorsal view of the skull of *H. horridum*, with enlarged figures of the grooved maxillary teeth, along with cross and vertical sections. They compare the teeth of *Heloderma* with those of *Varanus*, a python, and a rear-fanged snake, noting the similarities in structure. A year later Steindachner (1879) pointed out that the teeth of *Heloderma* were grooved, in contrast to those of *Lanthanotus*, which he had described the previous year, erroneously stating that the dentition was similar to that of *Heloderma*. Parenthetically it may be observed that little attention was given to this observation. Barbour (1926; revised edition, 1934), perhaps basing his assumption only on the belief that *Lanthanotus* is closely related to *Heloderma*, mentions that the Bornean lizard is strongly suspected of being poisonous. Shufeldt (1891c) observed that there was nothing on record to show this, and Kopstein (1926) stated definitely that *Lanthanotus* was not venomous. Nevertheless its inclusion by Camp (1923), Romer (1945), and others in the family Helodermatidae led many authors, Cuesta Terrón (1930) for example, to assume that the Bornean lizard must be venomous. Da Fonseca (1949) is uncertain, but does mention the possibility that *Lanthanotus* might be venomous. Kauffeld (1954) writes that "it is not known whether *Lanthanotus* is venomous."

EARLY EXPERIMENTS

While attention was at first largely directed to the grooved teeth, the widely quoted comments of Sumichrast (1864a) pointed out the desirability of making suitable experiments. Sumichrast reported that the natives considered the bite of *H. horridum* to be exceedingly dan-

gerous, dreading it as much as bites of the most venomous serpents, including the fer-de-lance (*Bothrops atrox*). While he believed that the gravity of the bite of the *escorpión* had been much exaggerated, he was not "absolutely disinclined" to believe that were the saliva of the creature introduced into the system, it "might occasion inconveniences." He wanted to carry out some experiments but had so much difficulty securing specimens not seriously injured that it was not until 1875 that Bocourt, in a note sometimes credited to Em. Blanchard, who presented it, reported the results of Sumichrast's crude investigations. Sumichrast (1880a, 1880b) later published his conclusion that animals "of a certain size" might occasionally die from the bite of *Heloderma*, but when young dogs were bitten there was no more than a slight swelling at the site of the wound.

Bocourt quotes from Sumichrast's earlier (1864a) paper, adding notes that were received from him along with specimens consigned to Bocourt from Tehuantepec. Sumichrast had experimented with a young *H. horridum*, inducing it to bite a hen on one wing and a cat on the leg. The hen died within 12 hours, with blood exuding from its mouth, while the cat resumed its normal activities the day after it was bitten, with symptoms no more severe than a swelling at the site of the injury to its leg. Sumichrast points out that these experiments are insufficient to prove conclusively that the lizard is venomous, but he is prepared to believe that popular notions concerning the lizard are not without foundation.

Sumichrast's reports, coupled with the previous descriptions of the grooved teeth, stimulated considerable interest in *Heloderma*, specimens of which were, however, not easily obtained for study. Most representatives of the species *H. horridum* that reached Europe were unsuitable for dissection, and relatively few specimens of *H. suspectum* had been obtained. Cope had named the latter in 1869, but in rather informal fashion, as the brief diagnosis is only the Secretary's (S. B. Howell's) summary of the account Cope had presented at the weekly meeting of the Academy of Natural Sciences of Philadelphia. Cope is quoted as stating: "though the lizards of this genus could not be proved to inflict a poisonous bite, yet that the salivary glands of the lower jaw were

emptied by an efferent duct which issued at the basis of each tooth, and in such a way that the saliva would be conveyed into the wound by the deep groove of the crown."

This brief note was overlooked by Gervais (*supra cit.*), as well as by Fischer (1882), who was the first to provide illustrations of the venom gland, depicting what he assumed were the efferent ducts leading from the gland through the mandible. In view of the fact that the ducts led only to the teeth in the lower jaw, Fischer attached significance to Sumichrast's report that when struck *H. horridum* "throws itself upon its back, this singular maneuver being repeated whenever the lizard is menaced."

This idea, namely, that the lizard must turn over on its back in order for the venom in the lower jaw to flow into the wounds produced, was later cited (Garman, 1891; George Wharton James, quoted by Snow, 1906; Woodson, 1944; and Hegner, 1935, for examples) in many popular accounts to explain the lack of any serious effects from bites inflicted on human beings and other animals. Fischer's account of the venom apparatus, along with his quotations from Sumichrast's reports, appeared the same year that several other notes were published. Fayrer (1882) is quoted as stating that he was present when two guinea pigs were bitten on the hind leg in an experiment carried out with a specimen of *Heloderma* in the zoological garden in London. Fayrer noted their symptoms but watched them for only half an hour, learning later that both of them died.

An unidentified writer (Anonymous, 1882b; presumably Cope, not B. J. D. Irwin as Woodson, 1947, indicates, nor "Dr. Irving" to whom Phisalix, 1917 and 1922, credits the note) mentions the addition of *H. horridum* to the zoological garden in London, adding that its venom was tested on a frog and a guinea pig, both of which died shortly after being bitten. The same writer reports that 15 years previously "Dr. Irwin, U.S.A., experimented with the *H. suspectum* in Arizona," and concluded that it was harmless. At approximately the same time Shufeldt (1882) was bitten by a captive Gila monster, suffering some ill effects, which he described in a brief note, to which Cope (1882) appended comments. Cope mentions Fischer's account of the venom glands and ducts, adding that he, Cope, had observed

them many years previously. Cope had forgotten whether he had published the information, but stated that it was this observation that led him to apply the name *suspectum* to the Arizona species. Cope was even more forgetful later, for in 1900 he quotes extensive passages from Shufeldt (1891d) after stating earlier in the same account that he could "detect no evidence of any poison glands."

Meanwhile a fair number of miners, prospectors, adventurers, and settlers had reached Arizona, and several museums and zoological gardens in the East, as well as in Europe, had obtained living specimens of *H. suspectum*. Shufeldt, perhaps having his interest whetted as the result of the bite he suffered, contributed several additional papers to the literature dealing with *Heloderma* during the following decade. The most important of these is his extensive account of the anatomy that appeared in 1890.

In this contribution Shufeldt reviewed the literature, citing 64 papers that had some bearing on his study of *Heloderma*. He commented on the relationships of the family and described many features of the anatomy, including the venom apparatus, of a female *H. suspectum* in detail. Misled by Fischer's earlier work, Shufeldt depicted the venom ("submaxillary") gland, showing what he thought were four ducts leading upward from the middle of the gland, "each to its opening on the outer surface of the mandible, where they entered." Shufeldt pictures the ducts as passing obliquely upward and inward through the lower jaw, opening within the mouth at the base of the individual teeth that were supplied with venom.

Immediately following the publication of Shufeldt's account of the anatomy, Boulenger (1891a) undertook a more detailed study of the osteology of both species of *Heloderma*, criticizing some of Shufeldt's findings and disagreeing with Baur (1890), who had correctly assigned the helodermatids to the Platynota. Boulenger's account was followed by that of Stewart (1891) who makes additional corrections to Shufeldt's paper, finding that the supposed ducts that passed through the bone of the jaw were in reality a dental nerve and associated blood vessels.

Stewart demonstrated that the inferior labial poison glands were altogether exterior to the

jaw, with the ducts passing directly from the gland to openings on the inner side of a fold of mucous membranes that intervenes between the lip and jaw. In *H. horridum* he found only one opening on each side, whereas in the gland of *H. suspectum* there were four or five openings on the mucous surface. (Fox, in Loeb *et al.*, 1913, found several openings in both species.) When Stewart dissected a fresh specimen under water, the slightest pressure on the venom gland forced a milky fluid from the ducts. The venom readily diffused in the water, but the mucus from other glands hung in the water as transparent ropy clouds. Stewart reported that the venom glands consisted of well-defined lobes, which in *suspectum* converge and partly fuse as they pass upward from the lower border to the anterior extremity of the lower jaw.

Shufeldt (1891a) replied to Stewart immediately, admitting that his figure and description depicting the ducts passing through the mandible were in error. He verified Stewart's account, but raised some pertinent questions: "Why are the upper teeth grooved when there is no poison gland in the upper jaw? Would not such a severe bite as *Heloderma* is able to give kill 'frogs and insects,' even were no poison injected into such wounds?"

Shufeldt asked an additional question, hedging on his statement of 1890, when he had observed that "Experiments made by a number of competent investigators during the past few years have satisfactorily demonstrated the fact to my mind that the venomous or non-venomous character of the bite of *Heloderma* is placed beyond the peradventure of cavil, for there can be no doubt now but that its bite is soon fatal, at least to the smaller kinds of animals. Whether it has ever proved fatal in the case of man I believe remains an open question, although I am inclined to believe that, too, will sooner or later be substantiated." For only a year later Shufeldt (1891a) asks, "Are the grooves on the teeth there to conduct a position into the wounds inflicted by the teeth of this lizard?" Without citing any basis for his views but completely reversing his stand of the previous year he states: "Here in America the evidence would seem to be rapidly leading to the demonstration of the now entertained theory that the saliva of this hereto-

fore much dreaded reptile is possibly almost completely innocuous."

Later the same year Shufeldt (1891c, 1891d) published two additional papers, again ignoring the statement in his paper of 1890, and citing only one paper (Garman, 1891) that he had not included in the extensive bibliography accompanying his general account of the anatomy of *Heloderma suspectum*. Shufeldt (1891d) mentions the earlier statements of Cope and of Gray concerning the grooved teeth, the conclusions reached by Sumichrast as the result of his crude experiments with *H. horridum* in México, and the opinions of Günther (1882) and Sclater (1882), both of whom believed that there could be no doubt concerning the poisonous nature of the bite of *Heloderma horridum*.

Of far greater importance were the experiments reported by Mitchell and Reichert (1883), summarized by Anonymous (1883), and M[artin] (1883) that Shufeldt discussed. Mitchell and Reichert extracted venom from *Heloderma suspectum* by allowing the reptile to bite on the edge of a saucer, finding that "a thick, fluid-like saliva dripped in small quantities from the lower jaw. It was slightly tinted with blood, due to the violence of the bite, and it had a faint, not unpleasant aromatic odor." The venom thus extracted was injected hypodermically into frogs, pigeons, and rabbits, all of which died in a few minutes.

These were the first scientific experiments to be carried out. They are accepted by Martin and others as the first conclusive proof that the lizard was venomous. Mitchell and Reichert compared the venom of *Heloderma* with that of snakes, asserting that it differed in physiological action, the venom from snakes acting on the respiratory center, while that of the Gila monster paralyzed the heart. The venom of *Heloderma*, they reported, caused no local injury when injected subcutaneously, but arrested the heart in diastole, from which conditions the organ passed into a contracted state. The heart muscle lost its irritability when other muscles and nerves still responded to stimulation. Snake venom they said, was acid in its reaction, in contrast to that of *Heloderma*, which Mitchell and Reichert said was alkaline.

These experiments by Mitchell and Reichert might have been expected to settle the controversy, despite the earlier experiments of

Sumichrast and the experiments said to have been carried out by Irwin. However, Yarrow (1888a) raised a dissenting voice. He was already on record (Yarrow, 1875; quoted also by Anonymous, 1879) as having stated that while the Gila monster was believed to be very venomous, "such is not the case; for although it will bite fiercely when irritated the wound is neither painful nor dangerous." Three years later Yarrow (1888b) quoted extensively from Mitchell and Reichert in an account of the Gila monster published in a handbook of medical sciences, despite the fact that he doubted whether "true poison glands actually do exist." In the same handbook he writes: "With regard to the very poisonous qualities of the *Heloderma* saliva, recent experiments by the writer would seem to indicate an extremely feeble toxic effect, at least so far as rabbits and fowls are concerned." Later in the same account he observes that there is conflicting evidence, but "opposed to the view of its [the Gila monster's] non-dangerous nature are the facts that persons have undoubtedly perished from its bite, the writer having in his possession the affidavits of two respectable individuals who witnessed a death."

Yarrow (1888a) published these affidavits in the introduction to his account of his own experiments that appeared the same year. Here it became apparent that there was some doubt concerning the cause of the deaths to which these affidavits referred. Both victims had consumed large quantities of alcoholic liquor, and one of them had died three months after being bitten. Noting, as had Shufeldt (1882), that Mr. Henry Horan of the National Museum had been bitten several times without serious effects, Yarrow again reviewed the work of Mitchell and Reichert, and described the experiments that he had carried out at the United States National Museum. This account merits more detailed review, not because Yarrow's experiments were well controlled, but because they illustrate the defects of investigations carried out at that time.

To extract venom Yarrow employed a technique that differed from that of his predecessors. He forced the lizard to bite a piece of "artist's gum" sufficiently resilient to preclude injury to the teeth. The flow of saliva was swabbed up with pledgets of absorbent cotton

that were washed out with glycerin, the saliva being preserved in the same liquid. However, extracted saliva was not used in all of Yarrow's experiments. The shaved legs of each of two rabbits were held in front of Gila monsters that were induced to sink their teeth into the flesh, in one to the bone. When examined the day following the experiments no apparent ill effects were noted except for slight lameness.

Next Yarrow injected three minims of the "solution of *Heloderma* saliva" into the leg of a hen described only as being "brown." Respiration was increased immediately after the injection, and remained so for an hour and three quarters afterward. The following day the fowl "appeared" to be entirely "recovered," and two days later Yarrow reports it as completely recovered. He explains that the chicken was a noisy one, and the increased respiration can be attributed to the fact that he had to "compress its throat" to prevent it from annoying other workers in the Museum.

In a second experiment with a hen described as being very thin, but healthy, even though it had been used in two experiments with rattlesnake venom, the dosage was increased to 10 minims of *Heloderma* saliva added to 10 minims of water, injected into the left breast. This time the fowl displayed an increase in respiration, ruffled feathers, drowsiness, and other symptoms, but six days later Yarrow pronounced it completely recovered, having "been so for several days." In a third experiment 25 minims of a solution of *Heloderma* saliva were injected into the left leg of another hen. This injection produced rather severe symptoms, with the chicken lying down, its mouth open, and respiration accelerated. These symptoms continued into the second day, with the fowl refusing food. On the fourth day it had completely recovered.

Far more drastic efforts were made to produce effects from the saliva in Yarrow's next experiment. He injected a total of 75 minims of the solution into a chicken, 25 into the breast and the same quantity into each leg. In a short time the fowl had a copious discharge *per anum*. Ten minutes later the chicken was lying down with its feathers much ruffled, and the next day it was found dead. However, Yarrow adds that the fowl was thin and weak, having been used in previous experiments, and sug-

gests that diarrhea produced by the glycerin rather than by the effects from saliva injected might have caused its death. He did not test the effects of glycerin alone. Because injections of the solution of saliva and glycerin produced such inconclusive results, Yarrow, after removing the feathers from the leg of a chicken, forced a large Gila monster to bite it, "with a copious flow of saliva and many lacerated wounds." Quite inexplicably Yarrow reports that the chicken seemed "perfectly well" the next day, with "no swelling or local manifestations whatever." Had the lizard bitten the fowl as described it would seem that the wounds inflicted could scarcely have been so completely healed the following day.

Yarrow's description of his work concludes with what he calls a "conclusive experiment." He collected 10 to 15 drops of fresh saliva by swabbing the mouth of a large Gila monster with a piece of absorbent cotton. The cotton thus soaked with saliva was inserted in an incision made in the breast of a chicken and allowed to remain. Two days later the chicken appeared perfectly well, and over a month later the wound had healed, with the cotton "encysted under the skin." Almost four months after the insertion of the cotton, the fowl was alive and healthy, with the cotton "still *in situ*." It was Yarrow's belief that "This experiment would seem to show that a large amount of *Heloderma* saliva can be inserted into the tissues without producing any harm, and it is still a mystery to the writer how Drs. Mitchell and Reichert and himself obtained entirely different results." In 1889 Yarrow published a somewhat abbreviated account of the same experiments without modifying his conclusions. However, Mitchell (1889) at the same time retained the views that he and Reichert had expounded in 1883. Van Denburgh (1898) later showed that glycerin either delayed the absorption of the venom or partly destroyed its effectiveness, which may account for Yarrow's conclusions.

Garman (1891), who cites the experiments of Sumichrast and the opinion of Shufeldt but not the work of Yarrow nor the experiments of Mitchell and Reichert, carried out additional crude experiments with a young cat. The mammal was bitten on the "right hand and wrist" by a Gila monster. The wound "occasioned some distress," but the kitten recovered, and

was subjected to two additional bites on the forearm 24 hours later. Two hours afterward, no longer paying any attention to its wounds, which it had been licking, the cat was killed and skinned in order to ascertain that the teeth had actually penetrated. Garman was satisfied that they had, and considered his experiments as having supplied "confirmation of the opinion that the species is venomous to a certain degree, to an extent, that, while it may most often prove fatal to very small animals, is only in exceptional instances deadly or perhaps even dangerous to larger ones. The effect on the kitten was identical with that on the puppies in Sumichrast's [1880a] experiments."

Investigations of the effects produced by the venom of *Heloderma* also attracted the attention of the practitioners of homeopathy. Their interest stemmed largely from their search for new drugs rather than from any desire to provide remedies for the bite of the Gila monster or the *escorpión*. It was the belief of homeopaths that disease is cured by substances that, on a healthy person, produce effects similar to the symptoms of the malady for which a cure is sought. Thus, according to their theory, if it could be shown that the venom of *Heloderma* produced symptoms similar to those of maladies already known, it might suitably be employed in their treatment. It was largely for this reason that accounts of the venom and its effects found their way into the homeopathic literature, to which Shufeldt (1901) later contributed, finally admitting, in view of the work of Van Denburgh and Wight, that the Gila monster was indeed venomous.

Anonymous (1890a), quoting letters received from Charles D. Belden, M.D., of Phoenix, Arizona, as well as newspaper clippings supplied by him, provides information concerning the effects of bites inflicted by the Gila monster. Belden, whose clippings also mentioned the work of Mitchell and Reichert, is quoted as having written that "This animal does not bite frequently, but when it does it is understood that the result is a benumbing paralysis like to *paralysis agitans* or to *locomotor ataxia*." This statement is evidently the basis for the suggestion by Anonymous, as indicated by the title of the article: "Gila monster (*Heloderma horridus*). A suggested remedy for paralysis agitans and locomotor ataxia." Clarke (1890)

also mentions the conclusions of Mitchell and Reichert, observing that the poisonous character of the lizard "has been scientifically established for only a very few years." Nevertheless, Bradford (1895), while citing Treadwell's (1888) report of a fatality from the bite of a Gila monster and with little basis for refuting the belief, titles his article "Is the Gila monster venomous?" Bradford cites the earlier papers concerned with the use of *Heloderma* venom as a drug, concluding that in it "we may have a valuable remedy for certain forms of paralysis."

LATER EXPERIMENTS

A decade before the turn of the century the evidence as well as opinion was in conflict, as Cope (1900) observes, quoting extensively from Shufeldt (1891d). It remained for Santesson (1897) to review the literature more critically and to renew the investigations of the venom. In conjunction with Santesson's work, Holm (1897) made the first histological examination of the venom glands. Santesson obtained the venom from *Heloderma suspectum* by inducing the lizards to bite into sterilized sponges or by applying pressure to freshly excised glands. His was a far more scientific investigation than any that preceded it. He employed precise methods and extended his investigation to deal with the physiological and chemical properties of the venom. When the venom was mixed with the blood of other vertebrates he found that it caused the red corpuscles to swell so that they lost their biconcave form and appeared to be smaller and spherical. He also tested the influence of physical and chemical agents on the venom, and the effect it had on the blood of the lizard from which it had been extracted.

Santesson injected the venom into frogs (*Rana temporaria* and *R. esculenta*), white mice, and rabbits. In frogs he observed a curare-like effect, with paralysis of the respiratory center two hours after injection of the venom. In mice dyspnea preceded respiratory failure, to which he attributed the death of the animals tested.

The same year that the reports of Santesson and Holm appeared, Van Denburgh (1897b) was quoted as having demonstrated that the

saliva of the Gila monster was poisonous, and that its bite would in almost every case cause death if the teeth of the lower jaw penetrated the skin. Van Denburgh's detailed account of his experiments was published the following year (Van Denburgh, 1898). After reviewing the conflicting statements then in print, he precedes his account of the 30 experiments he performed by raising the questions to be answered: "Is the bite of the Gila monster poisonous? If poison is present what are its physiological effects? What are the causes of such diversity of opinion?"

To extract venom Van Denburgh induced a Gila monster to bite filter paper wrapped around a piece of soft rubber, afterward dissolving out the saliva in water. Unlike Yarrow, Van Denburgh took the precaution of injecting other substances into pigeons to determine whether any of these produced effects when not in combination with *Heloderma* saliva. He first injected water in which filter paper had been soaked, then human saliva mixed with water, and finally the blood of a horned toad (*Phrynosoma*) mixed with water, without noting effects on the pigeon from any of these mixtures. He adds that a quantity of thick mucus is often present in the back of the mouth of the Gila monster, but that this is entirely without poisonous properties.

The solution of venom and water extracted from the paper was slightly yellowish or opalescent, often stained with blood from the lizard's gums. Like Mitchell and Reichert, Van Denburgh found the venom to be slightly alkaline (later in the same paper attributing the alkalinity to the harmless saliva with which it was mixed, "while a solution of the poison gland itself is quite neutral"), characteristically with a pungent though not unpleasant odor, that became less noticeable when the lizard was caused to bite every day. He describes two experiments in which 12 and 10 minims, respectively, of a solution of the venom in water were injected into pigeons. Death resulted in 11 minutes in the first pigeon, in 16.5 minutes in the second. There were no local effects, and in the first experiment the heart was beating regularly when death occurred. Van Denburgh mentions that a large number of other experiments were performed "in which death followed the injection of *Heloderma* saliva quite

as certainly and almost as quickly as when rattlesnake venom is used."

Van Denburgh then tested the effects of venom that had been boiled for "a few seconds," the result of his first experiment with a pigeon suggesting that the action of the poison was delayed. When he repeated the experiment with a dosage similar to that used in the previous experiments, this time boiling the solution of the venom for "about five minutes," a pigeon died in 21 minutes. He concluded that boiling had relatively little effect on the toxic properties of the saliva. On the other hand when a solution was allowed to stand for a few days an odor of putrescence indicated the effects of decay, and large dosages of such solutions produced no ill effects when injected into pigeons. Van Denburgh is careful to note, however, that his experiments with putrified venom were not conclusive, as he had neglected to test the solution while it was fresh. He made but one test to determine the effects of desiccating the venom, re-dissolving it in water, and injecting a very small dose subcutaneously in a pigeon. The bird exhibited symptoms similar to those injected with fresh solutions of the venom, but survived.

Van Denburgh also tried adding alcohol to the venom, which produced an opalescence ascribed to "a finely divided albuminous coagulate," which could not be removed by filtering the solution through paper. When the solution of undiluted venom was added to 95 per cent alcohol and injected into pigeons, they were killed virtually as promptly as when fresh venom was injected. Van Denburgh concludes that alcohol does not influence the action of the venom.

Quite different results were obtained when venom was dissolved in glycerin. Two pigeons survived injection with this solution, but a third one died. The results seem not entirely conclusive, but Van Denburgh states that "glycerine seems to dissolve the poison and to partly destroy its effectiveness, though this seeming injury may be due to the slowness with which glycerine is absorbed, preventing the poison from reaching the circulation rapidly enough to result fatally."

Fischer (1882), Shufeldt (1890), and Stewart (1891) had all observed the venom glands in the lower jaw, but failed to find simi-

lar structures in the upper jaw. Stewart commented on the presence of a few small mucous glands behind the venom gland, but mentioned none in the upper jaw. Prior to Van Denburgh's work no investigator had made any effort to distinguish between the excretions of the upper and lower jaws, most of them having employed techniques in extracting the saliva that made it difficult or impossible to be certain of the source of the saliva. Van Denburgh, by placing a sheet of rubber between two sheets of filter paper obtained the unmixed saliva from each jaw. He writes that "when thus obtained and dissolved in water, the saliva of the upper jaw is a yellowish liquid, usually more or less tinted with blood, slightly alkaline, without any odor and absolutely harmless at the very time when the lower jaw is flooded with the deadly venom." He found that the quantity of saliva obtainable from the upper jaw at any one time is only a little less than that obtainable from the lower, but that the saliva of the upper jaw is exhausted much more quickly than that of the lower with repeated extractions.

Van Denburgh carried out 14 experiments, in six of which he injected into pigeons the saliva from the upper jaw. In no instance does he report any ill effects. But in eight experiments conducted at the same time where saliva from the lower jaw was injected into pigeons seven of the birds died, and the eighth was quiet and drowsy for a time after the injection, even though it recovered. In one experiment all the saliva collected from the upper jaw was injected into a pigeon without causing the slightest ill effect, while one fifth of that obtained from the lower jaw at the same time caused death in a pigeon within 52 minutes.

To gain more precise knowledge of the sources of the fluids in the mouth, Van Denburgh removed the glands from the lower jaw, finding, as Stewart had reported, that when removed from its sheath each gland consisted of three or four distinct lobes, each emptied by a separate duct. The lobes vary in number because of the occasional union of the first and second or the presence at the rear of a small, isolated, ductless portion. Each of the four lobes was excised and soaked separately in water, from three to five minims of the resulting solution being injected into the breast

muscles of "a small finch." In each instance the bird died in approximately five minutes, whereas six minims of water injected into a similar bird produced no discernible effects.

Following his extensive experimental work and his careful post-mortem examinations of pigeons killed by the venom of *Heloderma suspectum*, Van Denburgh reviews the symptoms observed in pigeons following injections with the venom, namely, their loss of interest in their surroundings, their inability to control their equilibrium, their drowsiness, the accelerated but shallow breathing, and the partial paralysis that precedes an unconscious state that may or may not be followed by convulsions before death ensues. Following death the blood is very dark, and the heart is either beating or responds to mechanical stimulation. The arteries and usually the ventricles are empty, while the veins and auricles are full of blood, usually more or less clotted. No extravasation is noted in any of the organs, nor is there any discoloration at the site of the injection.

Drawing his conclusions from these observations, Van Denburgh writes that "it is very evident that death is due to asphyxiation," adding that this may be brought about (1) by the action of the poison on the nerve centers controlling respiration, (2) by the formation of blood clots in the veins, or possibly (3) by other effects, none of which was evident from the results of his experiments. His findings were not in agreement with those of Mitchell and Reichert, who had reported that death was occasioned by the action of the venom on the heart rather than from paralysis of the respiratory center. Van Denburgh suggests that such different effects can possibly be ascribed to the fact that he used venom that was more diluted than that used by Mitchell and Reichert.

With reference to the diversity of opinion that preceded his work, Van Denburgh believes that there are several reasons for the occasional failure of the Gila monster to inflict a fatal bite. Having demonstrated that the saliva from the upper jaw is harmless, he suggests that Shufeldt may owe his life to the fact that when he was bitten in 1882 only the maxillary teeth penetrated his thumb. Or the loss of several of the loosely attached teeth, the lack of any direct connection between the teeth and the venom gland, and the fact that the venom must

be forced upward into the wound may account for the failure of any venom to be introduced when a bite is inflicted. In view of the comparatively crude venom apparatus, Van Denburgh asserts that "the strange thing, then, is not that bitten animals should sometimes survive, but that they should sometimes die. Nevertheless—we must believe that a venom which can kill a pigeon in seven minutes and a rabbit in less than two might easily under favorable circumstances cause a wound to prove fatal even to man—a belief that is rendered far from improbable by the extraordinary virulence of the poison and the lizard's habit of holding on like a bulldog to whatever it bites."

Unaware of Van Denburgh's work, but cognizant of the diversity of opinion that had arisen in the United States, Dugès (1899) mentions an experiment performed by a friend who caused a young pig to be bitten by an *escorpión* without its producing any serious symptoms, and reports the results of experiments that he himself carried out in México with *Heloderma horridum*; an individual about 50 cm. long was allowed to bite the leg of a young pigeon, which died within four and three-quarters hours. However, a small amount of the saliva mixed with distilled water and injected subcutaneously into the thigh of a small bitch produced relatively minor symptoms, and a dog of average size that was bitten evinced minor effects for only a brief period. Dugès expressed the opinion that while the saliva of the *escorpión* possessed toxic properties sufficient to account for the beliefs of the Indians, their stories considerably exaggerated the dangers from the bite.

Meanwhile Van Denburgh had renewed his investigations of the venom of *Heloderma suspectum*. In collaboration with Wight (Van Denburgh and Wight, 1900), no fewer than 42 experiments were performed with dogs, cats, and frogs. Several improvements in technique may be noted, Van Denburgh having profited by the experience gained in his earlier investigations and having now seen Santesson's account, which evidently appeared while Van Denburgh's previous account was in press. Venom was injected in normal salt solution instead of being dissolved in water, respiration was recorded mechanically, and arterial pressure was recorded with a manometer. Venom

was extracted by inducing a Gila monster to bite filter paper or sometimes by allowing the lizard to bite directly on rubber, letting the venom drop into a small dish.

Van Denburgh and Wight sought to explain the conclusions reached by Van Denburgh (1898) and Santesson (1897), both of whom had ascribed the immediate cause of death to respiratory failure, in contrast to Mitchell and Reichert (1883) who asserted that death resulted from cardiac failure when the venom of *Heloderma* was injected into animals. Both Van Denburgh and Santesson had suggested that the discrepancy in results might be attributed to their having used smaller doses of venom than did Mitchell and Reichert. However, Van Denburgh and Wight now reported that respiratory failure always occurred before the heart was profoundly affected, even when enormous doses of venom were injected intravenously. Nevertheless "the diaphragm always responds after death to mechanical and electrical stimulation."

These authors could not substantiate Santesson's findings concerning the curare-like action of the venom. They found the irritability and conductivity of the motor cells and end organs unimpaired. When venom was injected into the dorsal lymph sac of a frog (*Rana pipiens*) the nervous system was profoundly affected, the skin becoming abnormally irritable. Merely touching it with a thread caused the frog to make violent efforts to escape. However, many of the effects observed in frogs were not discernible in the mammals tested.

Mitchell and Reichert had reported that repeated injection of crotalid venoms brought about accelerated respiration as a result of a sudden drop in blood pressure; they attributed this effect to stimulation of the vagus nerve. Van Denburgh and Wight carried out several experiments with dogs after severing the vagus on both sides, finding that the explanation suggested would not hold for *Heloderma* venom, as the respiration was accelerated just as it was in dogs with both vagus nerves intact. Peripheral stimulation of other nerves was not definitely excluded, but they believed that both the increased respiration and the gradual paralysis could be attributed to the direct action of the venom on the respiratory center.

There is no need to describe the experiments of Van Denburgh and Wight in further detail. Most of their results are confirmed by the later work of Loeb *et al.* (1913), and Van Denburgh (1922) evidently finds no reason to alter the conclusions that he and Wight reached in 1900. He quotes directly from their earlier findings without any important modifications, summarizing their conclusions concerning the physiological action of the venom of *H. suspectum* as follows:

"1.—The effects of Gila monster poison differ in no *important* respect from those of various snake venoms.

"2.—The poison appears to act directly upon the respiratory center, causing a quickening and then a gradual paralysis of respiration.

"3.—The heart also exhibits a period of increased activity followed by gradual paralysis. These cardiac effects are probably due to local action of the poison.

"4.—The vasomotor center shows no evidence of primary stimulation, but injection is immediately followed by a great fall in blood-pressure.

"5.—The great primary fall in arterial pressure is due to vascular dilatation—the central or peripheral origin of which has not been clearly shown. The gradual secondary fall is caused by cardiac failure.

"6.—The motor nerves, with their cells and end organs, remain entirely unaffected.

"7.—The sensory apparatus suffers an increase in irritability followed by a total loss. These changes proceed from behind forward, and are of central origin.

"8.—Coagulation of the blood is at first accelerated, then retarded. Serious thrombosis may doubtless occur. The blood may be rendered incoagulable.

"9.—The red corpuscles are often caused to become spherical, and the blood, at least outside the body, may be laked.

"10.—Death usually results from paralysis of the respiratory centers, but when artificial respiration is maintained death supervenes as the result of cardiac failure. Thrombosis must be regarded as a *possible* cause of death.

"11.—The secretion of urine is stopped. Frequent micturition is caused by the slow contraction of the bladder.

"12.—Oedema and slight extravasation are sometimes, though very rarely, caused by *Heloderma* venom."

RECENT EXPERIMENTS

Since the turn of the century there have been several notable investigations of the venom of *Heloderma*, particularly those of Phisalix (1911a, 1911b, 1912a, 1912b, 1914, and 1917, summarized in 1922), and of Loeb and his collaborators (Cooke and Loeb, 1908; Loeb and Fleisher, 1910; and Loeb *et al.*, 1913) summarized in an excellent non-technical résumé by Loeb in 1921. Calmette (1907) presents only a brief survey of the literature, mentioning the work of Sumichrast and of Van Denburgh and Wight. Snow (1906), having been bitten without ill effects and unaware of experiments more recent than those of Mitchell and Reichert, again raises the question of whether the Gila monster is venomous. Similarly brief reviews of the literature have been included in such accounts as that of Werner (1913), or more recently that of Storer (1931) and the general

account by Arrington (1930) that preceded it.

Woodson (1943a, 1943b, 1944, and 1950) in a series of popular accounts reviews some of the literature and mentions additional accounts of human injuries or fatalities resulting from the bites of Gila monsters. In 1947 Woodson briefly summarizes the results of his survey of case histories. Pawlowsky (1927) includes some original illustrations of the histological structure of the venom glands of *Heloderma*, but otherwise his account is largely a summary of the statements of earlier workers. Few other scientific investigations have been made since 1900, and most of the published information concerning the venom or venom apparatus is based largely or entirely on the investigations reported by Loeb and his collaborators or by Phisalix. The very extensive works of these authors should be consulted by those seeking detailed information. The following accounts attempt only to summarize their conclusions, except in the few instances where more recent experiments or descriptions supplement their data or conclusions.

VENOM APPARATUS

The venom apparatus of *Heloderma*, while primitive as compared with that of venomous snakes, involves somewhat similar structures. The venom is secreted within specialized salivary glands and discharged via ducts that lead to the vicinity of venom-conducting teeth. In both species of *Heloderma* the venom glands are situated in the lower jaw, unlike those of venomous snakes, in all of which such glands flank the skull behind the eye above the upper jaw, or in some genera (*Masticora* and *Causus*) extend from the sides of the head onto the trunk. In front-fanged snakes, proteroglyphs and solenoglyphs, each gland has but a single duct leading to the base of either or both of a pair of alternately functional tubular fangs; in *Heloderma* the gland is made up of lobes, each with its separate duct that delivers the venom to the inner side of a fold of mucous membrane between the lip and the jaw. Here the venom reaches the grooved teeth and is supposedly drawn upward in the furrows by capillary action, being carried into the wound at the time the teeth are driven into the flesh of the victim when a bite is inflicted.

While snakes are derived from the same stock (Varanoidea or Platynta) that gave rise to the helodermatids, it is noteworthy that among these reptiles there have been three independent trends in the evolution of glands secreting venom. In such non-venomous primitive snakes as the boids the superior labial glands, which lie between the skin and upper jaw, are weakly developed. In the more advanced aglyphs (and probably the pleuroglyphs, which have many of the teeth feebly grooved), with saliva that is mildly toxic, these glands are moderately well developed, and divided into lobules, each of which discharges by a separate duct leading to the base of the teeth. Several intermediate stages are represented in the Aglypha, with the species most advanced in this respect having the posterior part of the superior labial gland enlarged and somewhat differentiated. To distinguish this specialized portion of the superior labial gland in the Aglypha and Opisthoglypha, Smith and Bellairs (1947) refer to it as the parotid. In the rear-fanged snakes, usually those with the larger, more deeply grooved fangs, the parotid has ac-

quired its own fascial sheath, and its secretions are discharged near the outer base of the fangs in from one to three ducts. In contrast the toxic saliva of vipers, pit-vipers, cobras, sea snakes, and their allies is produced in quite different and more highly specialized venom glands. These may have evolved from the anterior portion of the superior labial glands, although no intermediate stages have been found in living forms (Smith and Bellairs, *supra cit.*).

Thus among reptiles mechanisms for the production of toxic substances that can be introduced into the flesh of prey or of enemies have evolved in three distinct ways: (1) in the proteroglyph and solenoglyph snakes with the venom discharged from the venom gland through a single duct that leads to the entrance lumen of tubular teeth at the front of the upper jaw; (2) in the opisthoglyph snakes with venom from the parotid gland discharged in from one to three ducts leading to the base of grooved teeth at the rear of the upper jaw; and (3) in helodermatid lizards, with three or four ducts from the inferior labial venom gland discharging its secretions on the inner side of mucous membrane that flanks the dental sacs investing the base of grooved teeth in the lower jaw.

The venom apparatus of snakes, while used secondarily as a means of defense, is generally conceded to have evolved primarily as a more efficient means of killing or subduing their prey. The far less perfected venom apparatus of *Heloderma* certainly plays no important role in the food-getting activities of these lizards, although it doubtless has survival value as a protective device.

THE GROOVED TEETH

The teeth of helodermatids have often been described simply as being long, conical, and grooved. Actually they are far more complicated structures, as demonstrated as early as 1873 by Gervais. Oudematt (1940) describes the teeth as well as the dentition of *H. horridum* in considerable detail. It is noteworthy that the largest, most deeply grooved teeth are those located nearest the openings where the ducts leading from the venom glands discharge the venom between the lip and the lower jaw. These teeth, especially the fourth to the seventh, counting from the front, are those most often

grooved at opposite sides, although the deepest furrow is always at the front. Also, as can be seen in figure 34, each groove is flanked by a sharp flange or cutting edge. Similar but less well-developed flanges are present in the venom-conducting teeth of cobras (Bogert, 1943a) and crotalids (Klauber, 1939b), where they have also been interpreted as reinforcement ridges. Such snakes, of course, have tubular rather than grooved fangs, and usually the cutting edges are present only near the tip of the fang, on the outer and inner edges. In *Heloderma* these flanges extend throughout most of the length of the tooth, terminating on the pedestal. Cross sections show the fang to be more nearly lance-shaped at the tip. Such fangs as those of *Heloderma* are probably more readily driven into the flesh of the victim than a simple conical tooth. Moreover, the cutting action would produce a wound in front of the groove where the venom could more readily flow or be drawn by capillary action than would be the case if the groove were located on the edge of a simple, elongated, cone-shaped tooth. The teeth near the middle of the lower jaw are, therefore, moderately well specialized for the introduction of venomous secretions into the wound.

As implied in the preceding description, not all teeth in the dentary of *Heloderma* are so well adapted to convey the venom. The groove at the anterior of the tooth is always deeper and more extensive than the one on the posterior, which may be absent, or poorly developed, more often in *H. suspectum* than in *H. horridum*. Grooves are usually, but not always, absent from the posterior surface of the maxillary teeth. At the front of the mouth the outer premaxillary teeth are sometimes feebly grooved on the inner side, but those near the center usually lack even a shallow furrow. (This description is based on an examination of six skulls of *H. horridum* and 12 of *suspectum*.)

The lower edges of the maxilla and the premaxilla comprising the tooth-bearing elements of the upper jaw are in the same plane, so that the bases of the teeth all lie at approximately the same level. The longest teeth fall near the middle of the maxilla, becoming progressively smaller towards the rear as well as towards the front of the jaw, with the smallest teeth near the middle of the premaxilla. As seen (see fig. 1

or fig. 31) from the inner side, the dentary in the lower jaw possesses a crescentic tooth-bearing area, with the longest teeth attached near the middle as in the maxilla. The four teeth at the middle of the jaw are subequal in size, but the teeth behind as well as in front of them are progressively smaller, so that a line drawn through the points marking the tips of the respective teeth would describe an arc.

Thus the smallest teeth are situated in the front of both jaws, with somewhat larger teeth in the middle of the upper jaw, and the largest teeth in the middle of the lower jaw. In a specimen of *Heloderma horridum* with a skull 60 mm. long the largest premaxillary teeth meas-

ure 2.3 mm., the largest maxillary teeth are 4.5 mm., while the large teeth in the dentary attain a length of 6.0 mm., all measurements being made from the base at the outer edge of the jaw to the tips of the teeth. The dimensions of comparable teeth in a specimen of *H. suspectum* with a skull 50 mm. in length are, respectively, 2.0, 3.2, and 5.0 mm.

The presence of relatively small, feebly specialized teeth at the front of the mouth has significant implications bearing on the nature of the bite inflicted by these lizards. If the reptile fails to engage the large teeth in the lower jaw, teeth that are not only more likely to be supplied with venom but better adapted for the

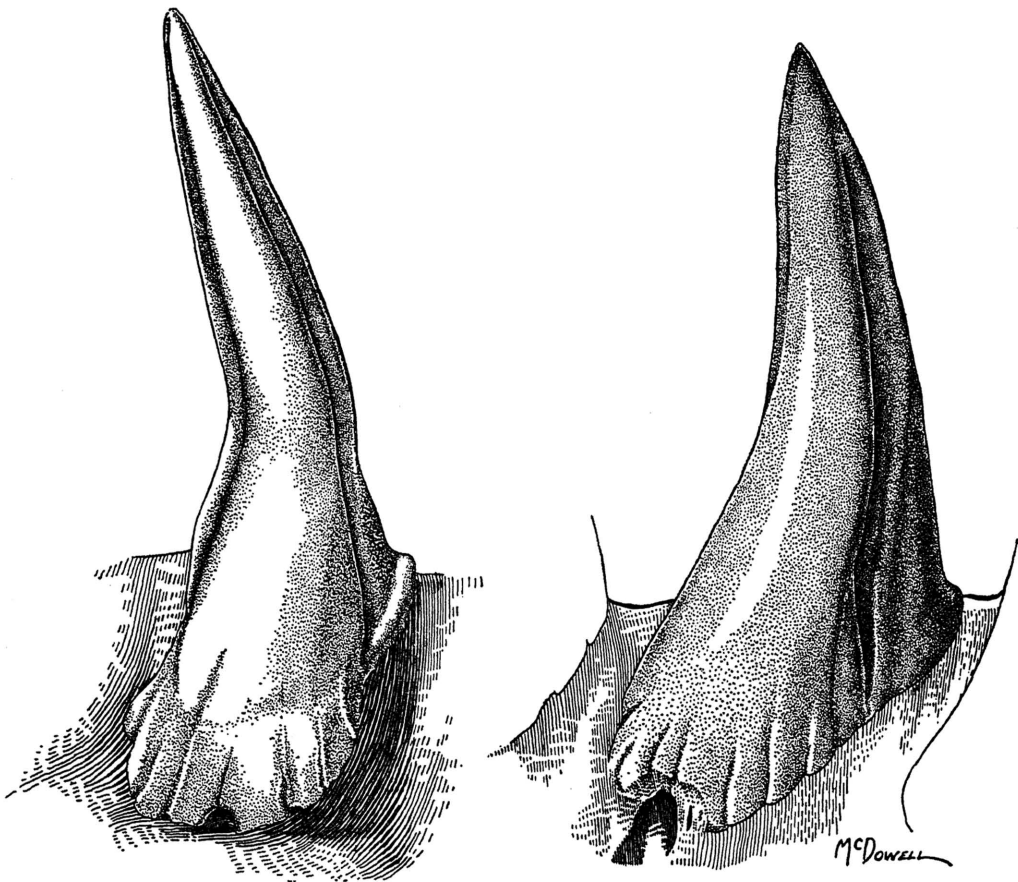


FIG. 34. Left: Lingual view of sixth mandibular tooth on left side of *Heloderma horridum*, showing cutting edges on both anterior and posterior surfaces, with groove on the anterior surface paralleling the edge. Right: Fourth mandibular tooth on left side of *Heloderma suspectum*, showing somewhat stouter tooth, with cutting edges less pronounced than on *H. horridum*, but with well-defined groove for conduction of venom. Drawings by S. B. McDowell.

purpose of introducing it into a wound, there is considerably less likelihood that poisonous secretions will be introduced into the flesh of the victim. The nature of the dentition is, therefore, enough to account for lack of symptoms in many human beings that have been bitten under conditions where the reptile engaged only the small teeth at the front of the jaws.

THE VENOM GLAND

The gross anatomy of the venom gland is depicted and described by Fox (*in* Loeb *et al.*, 1913), who corrected the errors of previous workers (Fischer, 1882; Shufeldt, 1890; and Stewart, 1891). Fox examined the gland in both species, finding them to be essentially similar. He describes the glands as follows:

"Each poison gland is of large size and is situated on the outer side of the anterior half of the lower jaw, immediately under the skin, from which it is separated by thin sheets of connective tissue. On the surface its position is indicated by a prominent swelling underlying the lower jaw.

"The gland is closely invested by a capsule of fibrous tissue. From the inner surface of this capsule septa extend into the body of the gland; the larger of these septa divide the glands into three or four primary subdivisions or lobes, while the smaller, which arise in part from the investing capsule and in part from the primary septa, penetrate the lobes and there form a network dividing them into numerous lobules.

"The lobes are the primary subdivisions of the gland. They vary from three to four in number and are arranged in longitudinal series. They increase in size from front to back. Each lobe is in reality a structurally independent organ, the different lobes being separated by complete fibrous partitions and opening by separate apertures to the exterior; they are bound into a compact whole by the investing fibrous capsule. In form they are roughly club-shaped, their upper excretory portions are narrowed, while their lower, glandular portions are rounded and swollen. Each lobe is a sac, containing a relatively large central excretory cavity, which narrows at its upper end to form a short excretory canal [or duct]. This canal opens on the outer side of the jaw close to the base of the tooth. The wall of the sac is of considerable thickness and consists of lobules

of glandular tissue. Numerous fine tabules, representing the intralobular ducts, open from the lobules into the central cavity."

The ducts discharge the venom at the outer side of the teeth, the place where the venom emerges being separated from the pedestals of the fangs by the outer wall of the dental sac, a cup-shaped fold of mucous membrane that invests the pedestal. External to the teeth is a shallow groove that is limited at the outer side by the more prominent fold of mucous membrane. This fold, according to Fox, is connected to the jaws by a series of vertical, obliquely transverse folds that lie in the regions between the teeth. These vertical folds interrupt the continuity of the groove and subdivide it into a series of shallow depressions, into the more anterior of which the ducts discharge the venom when the lizard is suitably stimulated.

These depressions are believed by Fox to serve as temporary reservoirs for the venom discharged from the gland. As the upper teeth project into these depressions when the mouth is closed, it may also be suggested that this arrangement provides the lizard with a means of getting venom into the grooves of the larger teeth in the upper jaw. The venom is carried into the grooves of the lower teeth solely by capillary action. If the tips of the grooved teeth in the upper jaw, particularly those near the middle, were introduced into pockets of venom in the depressions of the mucous membranes along the outer edge of the lower jaws, it seems possible that occasionally some venom might be carried into the grooves of the maxillary teeth in the same manner that it is drawn into the furrows of the opposing teeth.

The hissing, with the forcible expulsion of air through the mouth when a Gila monster or an *escorpión* is at bay, suggests further that such behavior may augment the dispersal of the venom within the mouth. Various authors (Barbour, 1926, for example) have commented on the frothy flow of saliva in Gila monsters that have been "teased" or otherwise stimulated. Under such conditions the venom, perhaps mixed with the non-toxic saliva from the upper jaw, might easily be carried to virtually all of the teeth, getting into the grooves of even those at the front of the mouth.

Shufeldt (1890) describes a tendinous expansion arising from the outer surface of the

superficial muscles near the posterior margin of the mandible and spreading out over the venom gland. Although it contains scarcely any muscle fibers, Shufeldt suggests that its contraction brings pressure on the encapsulated gland, forcing the venom out the ducts. Fox doubts that this is so, believing that expulsion of the venom is brought about by the tensions produced in the gland by the movements of the jaw. He found that such movements produced artificially in the dead animal result in the ejection of the venom.

The venom glands, while hypertrophied and specialized in their secretions, are not modified for the rapid expulsion of large quantities of venom at one time. It follows that the venom apparatus would be of little if any value in subduing prey. Such small creatures as juvenile rodents or lagomorphs, on which the *Gila* monster and its ally depend in part for sustenance, are manifestly killed by the crushing action of the jaws rather than by the action of the venom. Because it can be introduced into the flesh of an enemy, especially under circumstances that permit the lizard to retain its grasp for a prolonged period, the venom would, however, augment the effectiveness of the teeth as weapons of defense.

The histological structure of the venom gland, first described by Holm (1897) has since been studied by Phisalix (1912b, 1917, 1922), Fox (*in* Loeb *et al.*, 1913), and Pawlowsky (1927). Briefly summarized, each of the club-shaped lobes is a compound tubular gland occupied by a relatively large lumen, which Fox calls the central collecting duct. At its upper end it diminishes in diameter to form the excretory duct, with the discharge orifice at the apex of the lobe. Each lobe is divided into a number of lobules by septa from the investing capsule and the fibrous partitions separating the lobes. Each lobule is further divided into smaller lobules, with secondary septa penetrating in all directions, the subdivisions continuing until the terminal alveoli, each of which is separated from contiguous alveoli by a delicate septum, are reached. There is no sharp distinction between the terminal alveoli and the intralobular tubules, which are continuous. Each contains a lumen to conduct the secretions from the peripheral alveoli towards the central portion of the lobule, uniting with the lumina of other

lobules to form a few central tubules that open into the central collecting duct.

There are characteristic cells lining, respectively, the central collecting duct, the intralobular tubules, and the terminal alveoli. In the central duct the epithelium is one cell layer thick, comprised of columnar cells of somewhat smaller dimensions than those lining the intralobular tubules. Fox finds granulations in these cells, but agrees with Holm, who failed to find them, that the central collecting duct cells have no secretory function. The intralobular tubules are lined with columnar granule-secreting cells that are larger than those of the central collecting duct. The cells of the terminal alveoli are somewhat smaller than those lining the intralobular tubules, and cuboid in shape, rather than columnar. The large secretory granules present in the intralobular cells are lacking, although minute granules are present in the cytoplasmic reticulum.

Granules appear in the columnar cells and gradually increase in size to become the secretion granules. When fully formed they become detached from the cytoplasmic reticulum and come to lie within the vacuoles of the cell. The granules are dissolved within the vacuole, and discharged into the tubule when the inner membrane of the cell bursts. While there is no direct proof that the granules are the bearers of venom within the cell, or that they are even concerned in the production of the venom, the experiments carried out by Fox (*supra cit.*) strongly suggest that they do carry the venom or its precursor. Subcutaneous injection of pilocarpine in the *Gila* monster results in an increase in the secretion of the venom simultaneously with the rapid disappearance of the granules.

Fox and Loeb (*in* Loeb *et al.*, 1913) successfully transplanted portions of venom glands, inserting the excised portion within the muscles underlying the skin on the thorax. While the central portions of transplanted glands underwent necrosis and were replaced by connective tissue, the peripheral parts of the gland continued living for at least a month. In one instance tubules were observed alive after an interval of two months. Transplanted glands retained their toxic properties, although it was uncertain whether venom was secreted after the gland was implanted. Transplants were

equally successful whether made on the same animal from which the gland had been excised or on another individual. When an effort was

made to transplant part of a normal gland to a turtle, the latter died three days later, even though the gland remained quite normal.

THE VENOM

METHODS OF EXTRACTING VENOM

Mitchell and Reichert (1883) first extracted venom by causing helodermatids to bite on the edge of a saucer. Various methods have been employed by subsequent investigators, as noted in the historical résumé. Both Van Denburgh (1897b) and Santesson (1897) extracted venom from the excised gland. Gila monsters have been induced to bite sterile sponges, "artist's gum," sheets of filter paper, or rubber, as well as rubber encased in filter paper. Both Phisalix (1922, *et ante*) and Cooke and Loeb (*in* Loeb *et al.*, 1913) induced Gila monsters to bite a piece of soft rubber and with a capillary pipette drew off the secretion from the side of the rubber in contact with the mandibular teeth. Arrington (1930) recommends the use of a heavy rubber membrane and a medicine dropper. More recently Brown and Lowe (1955) describe a technique where the Gila monster is made to bite the rubber-covered rim of a stender dish so that the lower jaw is on the inside of the container. They state that teasing the animal usually intensifies the biting and chewing reaction, thereby increasing the venom yield. As much as 1.0 cc. ("1.0 ml.") of venom can be expected, they write, from an animal in excess of 300 mm. in snout-to-vent length. Brown and Lowe tried unsuccessfully to increase the yield by applying electrical stimulation to areas of the body and head, especially the lips.

Cooke and Loeb (*supra cit.*) observe that an animal in good condition will usually chew for several minutes, with a gush of venom each time the jaws close. The yield varies depending on the length of time that chewing continues, the condition of the teeth, which may be broken out so that the rubber is easily expelled by the tongue, or the time that has elapsed since the previous collection. Also when venom is extracted every day the quantity decreases rapidly, even when the lizards chew for prolonged periods. Sometimes no venom at all can be obtained after repeated extractions. Similarly, animals that have not eaten for some time yield

little or no venom, but there is a copious secretion after they resume feeding. Cooke and Loeb also suggest that the temperature may be a factor of importance and that animals kept for a considerable length of time in captivity gradually lose the power of secreting venom, but this seems doubtful if the lizards are maintained under suitable conditions. No mention is made of the size of the animal, although it is manifest that a large Gila monster can be expected to produce more venom than a juvenile.

Cooke and Loeb injected subcutaneously 0.1 grain of pilocarpine into a Gila monster in order to obtain greater quantities of venom after all that was obtainable had been extracted by simply inducing the animal to bite. The flow of venom began again after one to three minutes and lasted from 20 to 30 minutes, reaching a peak 10 to 15 minutes after the administration of pilocarpine. By such means the flow of venom could be increased three or four times, although it could not be maintained. Once pilocarpine had been injected, venom sometimes could be extracted with an injection on the day following. On the third day the injection of pilocarpine produced no result.

The quality of the venom is unaffected by the artificial stimulus to the glands induced by pilocarpine, according to Cooke and Loeb, who compared the strength of venom extracted with and without its use. They suggest that the failure of the venom glands to respond to a third injection of pilocarpine is owing to the exhaustion of the cells, which are unable to recover within 24 hours. They could not ascertain whether the drug, in addition to causing a secretion, was responsible for the discharge of venom from the glands. Pilocarpine also caused a discharge of urine and feces when first injected. Three animals subjected to more than three injections of this toxic substance died as a result.

VENOM YIELDS

Arrington (1930) says that as many as 40 drops (*ca.* 2 cc.) of venom have been extracted

from a single Gila monster in four or five minutes. Prior to administering pilocarpine Cooke and Loeb collected as much as 2 cc. of venom from Gila monsters of unspecified dimensions. This is twice the quantity that can be expected from lizards of the same species by means of the technique described by Brown and Lowe (*supra cit.*). However, the latter authors say nothing concerning variations in the secretion of venom, and the smaller yield they report may have resulted from their having collected venom from Gila monsters adversely affected by some of the conditions mentioned by Cooke and Loeb. That the technique for extracting venom advocated by Brown and Lowe is an improvement over that employed by Cooke and Loeb seems open to question. Removal of the venom with a pipette, as described by the latter authors, would appear to minimize contaminants more successfully than would be the case if the venom were allowed to flow into a stender dish. Two cubic centimeters may not be the maximum yield that can be expected from a large, healthy Gila monster, but no figures other than those cited are available. There can be little doubt that *H. horridum*, which attains greater dimensions as well as bulk, is able to secrete more venom at one time than its relative. No definite information concerning yields for the Mexican species is available.

PROPERTIES OF THE VENOM

Owing to the restricted distribution of helodermatids and the comparative rarity of serious bites inflicted on human beings, investigations of the venom of *Heloderma* have not kept pace with those of the venoms of the more widely distributed snakes, particularly those of the greatest importance from a medical standpoint. Many conclusions reached as a result of investigations of snake venoms carried out prior to 1930 have been subject to question or to reinterpretation within recent years. The literature dealing with venoms is controversial. In view of the complex biochemistry of most venoms difficulties are entailed in ascertaining their modes of action. Amaral (1954) observes that "Bio-assay for verification of the toxicity of active factors or purified principles in venom is still unsatisfactory." Porges (1953) has reviewed the recent literature dealing with snake

venoms, placing considerable emphasis on their enzymatic activity. Until the biochemistry of the venom of *Heloderma* has been investigated by more advanced techniques, the conclusions reached more than four decades ago must be accepted with reservations. Several enzymes have been recognized in snake venoms within the last two decades, and it is possible that such substances as hyaluronidase will prove to be present in the venom of *Heloderma* when it is reinvestigated.

Unlike snake venoms, which are mixtures, chiefly of proteins, the venom of *Heloderma* is believed by Loeb (1921) to be "not of a protein nature," although Loeb (*in Loeb et al.*, 1913) suggests that protein constituents may be present, and Alsberg (*in Loeb et al.*, 1913) mentions that the venom "contains a good deal of protein precipitable by acetic acid." However, Cooke and Loeb (*supra cit.*) report that the injection of the venom into an animal does not noticeably increase the susceptibility of the animal to a second dose of venom. The lack of any anaphylactic reaction tends to confirm the belief that at least the active principle of *Heloderma* venom may be somewhat simpler in structure than most proteins. The question cannot be answered with finality until a successful biochemical analysis has been made.

It should be noted that except for the crude experiments of Dugès, Sumichrast, and some by Cooke and Loeb carried out with the venom of *Heloderma horridum*, virtually all other investigations have dealt with the venom of *H. suspectum*. The effects of the venoms of the two species are evidently similar. As no careful comparisons have been made, however, it would be gratuitous to assume that they are identical.

A solution of the venom of *Heloderma suspectum* washed from filter paper is described by Van Denburgh (1897) as being slightly yellowish or opalescent. Arrington (1930) describes the venom as "whitish, varying in transparency with different individuals." Van Denburgh says that the venom had a pungent but not unpleasant odor; Arrington calls it "a peculiar medicated odor." Van Denburgh notes in his report that the venom is "faintly alkaline" but later that "the fluids of both jaws are decidedly alkaline, while a solution of the poison gland itself is quite neutral." Unless the venom is obtained from excised glands, it probably

contains fluid from the small mucous glands that Stewart (1891) mentions as being present behind the venom glands. The specific gravity of the venom seems not to have been ascertained. Phisalix (1917) mentions that when desiccated the venom loses approximately 85 per cent of its weight. It is readily soluble in distilled water or in physiological salt solution. Arrington reports the questionable observation that the venom "dries into crystals shaped similar to the crystals of Crotaline venom, but smaller."

Alsberg (*in* Loeb *et al.*, 1913), who unsuccessfully endeavored to isolate toxic principles of the venom, reports that it has a weak diastatic action and that it contains small quantities of lipase and pepsin. Diastase was present in the venom extracted from the live animal but was absent in the dried gland, suggesting that it is supplied from some other buccal secretion that becomes mixed with the venom.

Phisalix is not wholly in agreement with Cooke and Loeb (*supra cit.*), who carried out several tests with venom and report the following:

1. EFFECT OF HEAT: Boiled venom is as toxic as unboiled venom when the precipitate is not filtered off. Evidently some of the venom is carried down with the precipitate, which when mixed with physiological salt solution proves to be toxic when injected into an animal. As fresh venom can be heated to 100° C. without significantly decreasing its toxicity, according to Cooke and Loeb, it is possible to sterilize it before injecting it into experimental animals. This is of some practical importance in view of the fact that fresh venom often proves to be contaminated with bacteria. Venom boiled for 10 minutes can be used experimentally (but may lose its antigenic qualities; see below). However, there are advantages in sterilizing the venom by maintaining it at 60° C. for an hour. This produces a finer precipitate that more readily passes through a hypodermic needle of small gauge. Venom heated to 120° C. for 15 minutes is virtually as toxic as the fresh venom. Nevertheless there is a slightly injurious effect on the venom, perhaps due to the inclusion of some of the venom in the coagulum. Cooke and Loeb could not verify Santesson's (1897) statement that dried venom was less resistant to heat than the fresh venom. The venom of *Heloderma*

suspectum was found to be more resistant to the destructive action of heat than any of several venoms of crotalids, viperids, elapids, or hydrophiids tested.

Whereas venom exposed to higher temperatures appeared to retain its toxicity, experiments later carried out by Phisalix (1914, 1922) indicate that heat may have a destructive effect on an antigenic substance (or substances) contained in the venom. As a result of immunological tests she concludes that the venom of *Heloderma* contains at least two active substances. The action of each is wholly independent of the other. One containing antigenic properties is destroyed by exposure to a temperature of 80° C. for a period of five minutes or less, while the other is a toxin that resists the effects of heat.

2. EFFECT OF STANDING IN SOLUTION: No decrease in toxicity is noted when venom is allowed to stand for nine days when in physiological salt solution maintained under sterile conditions. However, venom that is sterilized and afterward merely covered becomes less toxic, presumably because sterility has not been maintained. Venom stored up to 21 days after sterilization loses some of its toxicity, but far less than unsterilized venom kept on ice. It is concluded, therefore, that unsterilized venom in solution loses its toxicity fairly rapidly because of bacterial action, whereas sterilized venom deteriorates more slowly, probably as a result of decomposition, according to Cooke and Loeb. Oxidation may conceivably play a part in the deterioration. The addition of thymol does not prevent the destruction of sterilized venom.

3. EFFECT OF DIALYZING: The venom of *Heloderma* passes through parchment paper rather slowly. Venom diluted to 10 times its original volume and put to dialyze against twice its volume of sterile salt solution evidently passed through the membrane so slowly that dialysis was incomplete at the end of a period of four and a half days.

4. EFFECT OF FILTRATION: The venom passes unchanged through a Chamberland filter (of unglazed porcelain through which liquid is forced under pressure; Cooke and Loeb do not specify which grade, although the one ordinarily used permits only particles smaller than 2 μ to pass). In this respect the venom of *Heloderma* resembles that of elapid more closely than

that of viperid snakes, as the venom of vipers does not pass through such a filter.

5. EFFECT OF ACID: Either fresh or dried venom, normally neutral in reaction, is unchanged in toxicity by the addition of acid (tested only with hydrochloric acid).

6. EFFECT OF ROENTGEN RAYS: The toxicity of venom is unaffected when the venom glands are exposed to Roentgen rays 10 minutes every other day for a period of about three weeks.

BACTERIAL CONTAMINATION OF VENOM

The saliva of 10 Gila monsters was examined by Rivas (*in* Loeb *et al.*, 1913) who reports finding "*Bacillus coli*" [= *Escherichia coli*] in five individuals after a single examination. Rivas believes that repeated examination of the lizards would have disclosed the same or-

ganism in most if not all of the lizards. Besides *E. coli* and "*B. pyocyaneus*" [= *Pseudomonas aeruginosa*], other pathogenic or pyogenic bacteria were found. Cultures were obtained from smears made at the point of inoculation of a guinea pig that had died from an intraperitoneal injection of fresh venom. One culture was found to be so virulent that scrapings from a 24-hour agar culture dissolved in sterile salt solution produced death in a guinea pig three hours after it was injected peritoneally. Rivas observes that such virulent strains may be a possible source of error in studies of reptile venoms. It may be added that the presence in *Heloderma* venom of pathogenic organisms may also account for some of the symptoms that have been noted in reports of bites inflicted on human beings.

EFFECTS OF VENOM ON ANIMALS; MINIMUM LETHAL DOSES

Venom glands presumably have arisen in reptiles in response to a need for increased efficiency in obtaining food or in combating predators. The precursors of such glands produced only mildly toxic substances that presumably were of aid in digestion. The advantages conferred on reptiles adapted to subdue their prey or to combat predators by means of their venom apparatus have seemingly led towards further specialization. Because natural selection usually operates in favor of increased adaptation to a given mode of existence, it seems probable that to fulfill its particular needs each species has become further specialized in its venom glands and their secretions. It can scarcely be fortuitous that the venom of such non-ophiophagous reptiles as rattlesnakes, which prey largely on lizards and mammals, is almost wholly ineffective as a means of killing snakes. In contrast the venom of such snakes as *Micrurus* that habitually prey on other snakes is quite toxic to such reptiles. No thorough study has been made, but the information available suggests that other species specialized in their feeding habits may have venoms that are particularly effective as a means of killing one sort of animal.

Because the venom apparatus of *Heloderma* appears to have evolved as a protective device, the venom might conceivably be especially toxic to those groups of animals that include potential

predators, principally mammals, birds, and reptiles. It does not follow that other animals are necessarily immune or that there is a precise correlation of toxicity with predator relationships. However, the venom of virtually every animal that has been tested has proved to be less toxic for some groups of animals than for others.

Cooke and Loeb (*supra cit.*) tested a number of animals, in addition to those employed in experiments by Mitchell and Reichert (1883), Santesson (1897), Van Denburgh (1897), Philalix (1912a), and others. The results obtained suggest that the venom of *Heloderma* is more toxic to the higher animals than it is to the simpler forms. The following account summarizes the results of these investigations, particularly those of Cooke and Loeb.

INVERTEBRATES

Several animals, including jellyfish, starfish, worms, snails, and the horseshoe crab, were injected with venom by Cooke and Loeb. All invertebrates tested appeared to be immune to the venom of *Heloderma*, or at least vastly more resistant to the venom than any vertebrate animals. Fertilized sea urchin and starfish eggs continued to develop and form swimming gastrulae when placed in sea water containing 3 to 7 per cent of venom.

VERTEBRATES

Cooke and Loeb carried out experiments to ascertain whether the method of administering venom influenced its toxic effects. They report that venom acts most quickly when administered intravenously, less rapidly when injected intraperitoneally, and still more slowly when injected subcutaneously. They obtained conflicting evidence from subdural injections and suggest that injection of large quantities of liquid into the subdural spaces may of itself have some injurious effect. When venom was injected directly into the stomach or the small intestine of a guinea pig no effects due to the injection could be noted. However, it is uncertain whether the venom is changed by the gastric or intestinal secretions or absorbed by the contents of the digestive tract.

Despite the fact that Cooke and Loeb note that the method of administering venom influences its effect, they do not indicate how venom was injected into the animals used in their tests. Presumably it was injected intravenously. They recorded minimum lethal doses of dissolved dry venom, observing that fresh venom varies in its toxicity. They found considerable variation in resistance among animals of the same species, especially when tests were made with fresh venom. Deviations from the mean were always towards a reduced resistance. While Cooke and Loeb state that they "did not find individuals showing more than average resistance," this statement evidently should not be taken too literally.

The conclusions of Cooke and Loeb are not always in close agreement with those of Phisalix, even when the same species were tested. Discrepancies in their results or conclusions can perhaps be attributed to differences in technique, as well as to individual variation in the animals tested, especially in those instances where experiments could not be repeated with several individuals of the same species.

FISHES

Only one fish, *Fundulus majalis*, was tested. The minimum lethal dose was 0.1 cc. of fresh venom for a fish weighing roughly 30 grams. Cooke and Loeb estimate the lethal dose as approximately 3 cc. per kilogram of weight.

AMPHIBIANS

Mitchell and Reichert (*supra cit.*), Santesson (1897), and Van Denburgh and Wight (1900) employed frogs in some of their experiments, but the only precise figures are supplied by Phisalix (1922) and by Cooke and Loeb. The latter authors tested five frogs, *Rana pipiens* and *R. clamitans*. Frogs weighing 80 to 85 grams and injected with 4, 5, and 6 milligrams of dry venom all died; one frog weighing 84 grams survived injection with 5 milligrams of venom, as did two slightly smaller frogs that received 3 milligrams of venom. Four milligrams is estimated as approximately the lethal dose for a frog weighing 80 grams. Tadpoles were more susceptible to venom than adult frogs. The lethal dose for a kilogram of tadpoles would be between 12 and 25 milligrams, whereas 50 milligrams of dried venom would be required to cause the death of a kilogram of frogs. Phisalix (*supra cit.*) indicates 350 milligrams of dry venom per kilogram as the minimum lethal dose for an unspecified species of frog.

A toad, *Bufo terrestris americanus*, proved to be more resistant to the venom than the frogs tested by Cooke and Loeb. An animal weighing 50 grams was killed by an injection of 15 milligrams of dry venom. In terms of body weight the lethal dose for this toad would be approximately 300 milligrams of venom per kilogram. Cooke and Loeb note that the toad is far more resistant to the venom of *Heloderma* than any of the endotherms tested, including the rat, which proved to be more resistant than other mammals.

REPTILES

Turtles tested by Cooke and Loeb include the painted turtle (*Chrysemys picta*), the spotted turtle (*Clemmys guttata*), the stink-pot (*Sternotherus odoratus*), and the common mud turtle (*Kinosternon subrubrum*). All reacted in approximately the same manner; 5 milligrams of dry venom were found to be sufficient to kill a turtle weighing 80 grams. The lethal dose for turtles was estimated to be 65 milligrams of dry venom for each kilogram of body weight.

Crocodylians have not been subjected to scientific study as far as the effect of *Heloderma* venom on them is concerned. However,

Bendire (1887) mentions that a small alligator, doubtless *Alligator mississippiensis*, died after being bitten by a Gila monster.

Lizards have been tested by Phisalix (1922) who injected an ocellated lizard (*Lacerta lepida*) weighing less than 30 grams with 0.8 milligram of venom or 26.6 milligrams per kilogram of the lizard's body weight, finding that it recovered within two hours. The green lizard (*Lacerta viridis*) was more resistant; one weighing 20 grams displayed no apparent symptoms after being injected with 1 milligram of venom. Phisalix concludes that the minimum lethal dose for *L. viridis* is more than 50 milligrams per kilogram of weight.

The only lizard tested by Cooke and Loeb was the Gila monster, which as are other venomous reptiles is markedly resistant to the venom of its own species.¹ The injection of enormous quantities of *Heloderma* venom might produce ill effects if injected into a Gila monster, but, in the words of Cooke and Loeb, "*Heloderma* shows a resistance to its own venom which for purposes of protection at least is complete." These investigators injected 2.25 cc. of fresh venom into Gila monsters weighing 500 grams. This is a quantity sufficient to kill 45 guinea pigs each weighing 500 grams. Such huge doses produced no apparent symptoms in the Gila monsters. Brown and Lowe (1954), apparently not cognizant of earlier investigations, repeated the experiment, finding that Gila monsters were unaffected by injections ranging from 0.20 cc. to 0.53 cc. of fresh venom.

Cooke and Loeb could not account for the resistance of *Heloderma* to the toxic effect of its own venom, but suggest that it may be explained by the remarkable adsorptive power of the liver, the kidneys, or other organs that ex-

erted a specific adsorptive action when tested with the venom. They mixed the serum of *Heloderma* with its venom, finding that the venom did not lose any of its toxic power. Consequently they conclude that the resistance of the Gila monster to its own venom is not due to the presence of antibodies in the serum. However, Tyler (1946, 1954) disputes these conclusions, reporting that the serum of *H. suspectum* is capable of neutralizing the venom of the same reptile. He found auto-antivenin in the liver extract, but not in extracts of the venom gland, pancreas, spleen, or kidney. Neither did he find antivenin in the serum of the rabbit or the chuckawalla (*Sauromalus obesus*). Antivenin was present in the globulin fraction of the serum of *Heloderma*.

Snakes have been tested by Cooke and Loeb as well as by Phisalix (1922). The former authors injected 35 milligrams into one garter snake (*Thamnophis sirtalis*) weighing 80 grams, and 25 milligrams into another snake of the same species but of unspecified weight. "Only one died after a second injection of similar quantity. The lethal dose of venom for snakes appears to be approximately 400 mg. pro kilogram of body weight." Phisalix states that 3 milligrams of dried venom is sufficient to cause the death of a viper (*Vipera aspis*) within 22 hours, and she estimates the minimum lethal dose as 40 milligrams per kilogram of body weight. Woodbury (1928) and Arrington (1930) mention rattlesnakes (*Crotalus*) killed by captive Gila monsters, but it is uncertain whether the snakes died from the effects of the venom or the crushing action of the jaws.

BIRDS

Van Denburgh (1897) employed "a small finch" in some of his experiments. One bird died within 3.5 minutes from the effects of 3 minims of *Heloderma* venom injected into the breast muscles. Several of the earlier investigators carried out crude tests with domestic fowl, as noted in the historical résumé. Pigeons were the least resistant of all endotherms tested by Cooke and Loeb. The minimum lethal dose for birds weighing an average of 250 grams was calculated as being 0.8 milligram of dried venom or 0.02 cc. of fresh venom. Phisalix

¹ This has sometimes been disputed, largely on the basis of the crude experiments of Nichol, Douglas, and Peck (1933), who took no precautions to exclude bacterial contamination of the venom employed. Also they carried out their experiments under conditions in which rattlesnakes (*Crotalus atrox* and *C. molossus*) were exposed to air temperatures as high as 100° F. Contrary to the assumptions of these authors, such reptiles are not exposed to these thermal levels for prolonged periods in their natural habitats. The accelerated action of bacteria at such temperatures may account for the supposed effects of the venom.

(1922) injected in aqueous solution 0.8 milligram of dried venom into the pectoral muscles of a sparrow, finding that this was sufficient to cause its death within 10 to 15 minutes.

MAMMALS

One insectivore, the European hedgehog (*Erinaeus europaeus*), has been tested by Phisalix (1912a, 1922). An individual weighing 570 grams injected with 19 milligrams of dry weight of venom in solution survived for only 24 hours. Phisalix estimates the minimum lethal dose for the hedgehog as 33 milligrams per kilogram of body weight.

The usual laboratory rodents have been used in experiments. Phisalix reports that a gray mouse weighing 15 grams survived injection with 0.26 milligram of venom; she estimates the minimum lethal dose to be over 16 milligrams per kilogram of body weight. Cooke and Loeb estimate the minimum lethal dose for a mouse of the same weight as 0.005 cc. of fresh venom, or 0.15 milligram dry, or 10 milligrams per kilogram of body weight. Rats were more resistant according to Cooke and Loeb, who indicate that the minimum lethal dose for a rat weighing 125 grams is 5 milligrams, or 40 milligrams of dried venom per kilogram. Phisalix apparently found young rats weighing 52 grams to be less resistant, as she calculates the minimum lethal dose as only 7.70 milligrams per kilogram of body weight. Cooke and Loeb found the minimum lethal dose in terms of body weight for guinea pigs to be the same as that for the mouse, animals weighing 500 grams being killed by doses as small as 5 milligrams. Phisalix reports that a guinea pig the same weight lived for only eight hours after having been injected with 3 milligrams, and she estimates the minimum lethal dose as 6 milligrams per kilogram.

Of the lagomorphs, only the rabbit, presumably domestic, has been tested. Whether there are differences between strains, or whether other factors affected the results reported, cannot be stated. Cooke and Loeb found the minimum lethal dose for a rabbit weighing 1500 grams to be 18 milligrams of dried venom, or 0.05 cc. of fresh venom; or, in terms of venom per kilogram of body weight, 12 milligrams and 0.04 cc., respectively. In contrast, Phisalix, who injected rabbits of the same weight, found that death resulted when as little as 10.8 milligrams

were used. She calculates the minimum dose to be 7.70 milligrams per kilogram of body weight.

Among carnivores, only the domestic cat and dog have been tested. Van Denburgh (1897) and Van Denburgh and Wight (1900) employed dogs in several experiments, noting their symptoms, but not estimating minimum lethal doses. Cooke and Loeb give the average weight for an unspecified number of dogs as 10,000 grams. Doses of 0.1 cc. of fresh venom, or 100 milligrams of dried venom, administered to such dogs resulted in their death. They indicate that the minimum lethal dose for dogs is 0.01 cc. of fresh venom, or somewhat more than 10 milligrams of dry venom per kilogram of body weight. A cat weighing 3000 grams died as a result of the injection of 0.9 cc. of fresh venom, or 0.3 cc. of fresh venom for each kilogram of weight.

No primates have been subjected to experimental test to determine the effects of the venom of *Heloderma*. Where human beings have been bitten it has been impossible, of course, to ascertain how much venom was introduced into the blood stream. Loeb (1921) doubts that it is possible for a helodermatid to inject a sufficiently large quantity of venom to cause the death of a human being. "Knowing the lethal dose for animals," he writes, "we can figure out that it would be necessary for the Gila monster to introduce at least half of a cubic centimeter of venom into the wound in the process of biting, in order to kill an adult, but probably a much greater amount would be needed." In contrast Phisalix (1922), who was herself bitten by a Gila monster of 520 grams that was 40 cm. in total length, has considerably more respect for the venom. She estimates the lethal dose for man to be in the neighborhood of 5 milligrams of dry venom. As tabulated by Phisalix, 5 milligrams of dried venom could be expected to cause the death of a man weighing 60 kilograms within an hour's time.

If Phisalix is correct in her estimate, human beings are less resistant to the venom of *Heloderma* than any other vertebrate tested, for the minimum lethal dose would be only 0.0833 milligram of dried venom per kilogram of body weight. This estimate is probably low. It is premised on the quantity of venom that a Gila monster can produce at any given moment and

the fact that a bite can lead to death. Phisalix concludes, "*Les nombreux prélèvements opérés sur six individus bien portants, nous ont fourni la moyenne de 5 milligr. par sujet.*" Her account does not indicate who the six individuals were who supposedly died from the effects of the venom. She cites the account of Treadwell (1888), who sent a clipping from the Cochise Record to Sir John Lubbock. The clipping mentions the death of a Colonel Yeager and includes the statement that "this is the third or fourth death which has occurred in the Territory [of Arizona] from the bites of this reptile." Other fatalities were on record at the time Phisalix wrote, and accounts such as that of Anonymous, 1893 (which Phisalix erroneously credits to Garman), report other deaths from the Gila monster. She may have had these in mind. Her estimate of the minimum lethal dose for human beings is open to question on other grounds, because she bases her deduction on "*la quantité de venin qu'un animal peut pro-*

duire à un moment donné." The quantity of venom that a Gila monster can produce is undoubtedly much more than it can succeed in injecting into a wound with its relatively crude venom apparatus. During a period of 15 minutes as much as 2 cc. of venom can occasionally be extracted from a large Gila monster, according to Cooke and Loeb, but there is no assurance that more than a fraction of this amount would be introduced into the blood stream of the victim. The length of time that the lizard is allowed to retain its grip would have a direct effect on the quantity of venom that penetrated the wound. It is not always an easy matter to disengage the jaws, and some time might be required if a Gila monster seized a man's wrist, as reported by Anonymous (1893). Death has been the outcome of a sufficient number of bites reported to leave little doubt that human fatalities can occur. However, Phisalix' estimate of the minimum lethal dose is based on assumptions that are difficult to substantiate.

PHYSIOLOGICAL EFFECTS OF THE VENOM

Mitchell and Reichert (1883) concluded that the venom of *Heloderma* affected the heart, arresting its action. Later investigations by Santesson (1897), Van Denburgh (1898), Van Denburgh and Wight (1900, summarized by Van Denburgh, 1922), Phisalix (1911a, 1911b, 1922), Cooke and Loeb (*in* Loeb *et al.*, 1913, summarized by Loeb, 1921) failed to confirm their findings. The latter authors are in general agreement that the venom affects mainly the central nervous system, with death resulting largely if not entirely from respiratory failure. The conclusions reached by Van Denburgh and Wight are quoted above in the historical résumé. Phisalix (1922) described the physiological effects of the venom on amphibians, reptiles, birds, and mammals, summarizing the results of investigations carried out since the early efforts of Sumichrast were reported by Bocourt in 1875.

Phisalix, having been bitten by a Gila monster, had first-hand knowledge of some of the symptoms produced by the venom of the creature. As the result of her experience, as well as of her work with experimental animals, she summarized the symptoms of envenomation. A free translation of her account follows:

"Were only the action of the venom on the lower vertebrates considered, it would be difficult to distinguish the action of the venom of *Heloderma* from that of the venom of the viper and of the mucous venom of the amphibians: pain, numbness, hypersecretion of the glands, paralysis of the respiratory system and heart, the first sign of impending death, mydriasis [dilation of the pupils]; we have found the same symptoms in warm-blooded vertebrates, in addition to some others; these may be summarized in their entirety, as follows:

"The local pain is shooting, radiating, and persistent; it is not lessened by the numbness that occurs almost immediately. The following symptoms appear: salivation, urination, defecation, vomiting (in the dog after intravenous injection), profuse sweating in man, dilation of the pupil, followed by weakened breathing and then respiratory paralysis that, judging from the experiments of Van Denburgh, can be the cause of death in the dog.

"The weakened respiration is accompanied by cardiac paralysis, with the heart arrested in diastole. According to Weir Mitchell the action of the heart is arrested prior to respiratory paralysis.

"Muscular paralysis is followed by asthema [weakness], and marked hypothermia, such as occurs in viper envenomation.

"Paralysis of the heart is followed consecutively by dizziness, fainting spells, occasionally accompanied by convulsions, and a sudden, then a progressive lowering of the arterial pressure.

"The edematous swelling, of characteristic color, that follows the bite of the lizard or inoculation of its venom, is always rather circumscribed and is not to be compared to the intense and spreading hemorrhagic action that characterizes the venom of viperids (*Vipera aspis*, *Crotalus durissus* . . .), but it is more marked than the colorless edema following the injection of cobra venom.

"In most warm-blooded vertebrates, the blood is greatly affected; it is hemolyzed, as much *in vivo* as *in vitro* (dog, rabbit, guinea pig, sparrow), hemolyzed *in vitro* in the case of man (hemolysis *in vivo* has not been investigated), while the corpuscles of cold-blooded vertebrates are not modified.

"Coagulation undergoes diphasic variations: it is first accelerated, then delayed; if the first action is severe enough one can have thromboses, as with the venom of viperids.

"Non-fatal envenomation brings on such secondary phenomena as a conspicuous emaciation that in a short time can result in the loss of as much as a fifth of the initial weight, as we observed in the hedgehog, and as Sumichrast observed in the cat."

Cooke and Loeb (*supra cit.*), following experiments with over 360 mammals and birds, enumerate the effects of the venom on endotherms; their interpretation of their results differs in some respects from that of Phisalix. They write that "when a warm-blooded animal receives a lethal dose of heloderma venom the first conspicuous effect is a disturbance of respiration. The breathing becomes quickened and the respirations are forced. After a time the respiratory rate diminishes and the respirations grow shallow; finally they occur only at long intervals, until after a period of respiratory spasm they cease altogether. Meanwhile other symptoms appear. The animal shows weakness and falls down, and frequently, though not as a rule, has acute attacks of convulsions. Reflex irritability becomes increased so that a slight

sensory stimulus is able to inaugurate an exaggerated response which resembles the response obtained in an animal poisoned by strychnine. The hind legs hang as if paralyzed. If the skin of the leg be pinched, however, a response is elicited, and this response may still be obtained very shortly before the last respiration. The corneal reflex may be obtained even later than the sensory skin reflex."

Cooke and Loeb found that respiratory disturbances were substantially the same in all warm-blooded animals, and "it is to the interference with respiration that we must attribute the immediate cause of death" in such creatures. Other symptoms were noted. When mice were injected subcutaneously in the thorax with lethal quantities of venom, one hind leg sometimes became paralyzed and spastic when the other hind leg was incompletely paralyzed. Pinching the skin or pricking the spastic leg produced no response, although if the entire leg was pinched a slight muscular response was sometimes noted in the other leg. Similar symptoms were noted in other mammals, but were more conspicuous in some species than in others.

Disturbances not common to all mammals but present in some include vomiting accompanying the discharge of urine and feces in cats and dogs, with a copious flow of saliva and tears. In cats a noticeable symptom was the loss of voice; no sound accompanied their crying movements. Rabbits and guinea pigs often developed an extreme rigidity of the abdominal walls, and occasionally there was a copious discharge from the tear ducts.

Cooke and Loeb suggest that the effect on the heart reported by Mitchell and Reichert resulted from their injection of very large doses of venom. This procedure might have caused "a reflex stopping of the heart." When Cooke and Loeb administered smaller but lethal doses they found that the heart continued to beat after respiration had ceased, for 10 to 30 minutes in endotherms and for several hours in frogs. The auricles continued to beat after the ventricle had stopped. Occasionally the cardiac rhythm was disturbed, with the auricles beating more often than the ventricle. Heart action was not always stopped in diastole; sometimes it was in systole.

While some swelling may appear at the site of a bite, the investigations of Loeb *et alii* indi-

cate that this is not due to the toxic principle of the venom. Such effects may be the result of mechanical injury from the extraordinary crushing action of the jaws, from the action of pathogens, from an admixture of other secretions from the lizard's mouth, or from a combination of these effects. The forcible removal of the lizard's jaws may, of course, entail additional injury, particularly when the reptile has grasped a digit, sinking in its teeth. When sterile venom was injected under conditions where bacterial contamination could be avoided there was no swelling or hemorrhage at the site of injection.

Post-mortem examination of animals killed by injections of venom revealed congestion and edema in the lungs. At times the liver, spleen, kidneys, and adrenals showed congestion, but these effects were not invariable and never so obvious as the congestion in the lungs. However, the most conspicuous and common macroscopic changes to be seen after death are in the alimentary canal. These are particularly marked when there was a considerable lapse of time between the injection and death. The intestines are greatly dilated with fluid and gas. In guinea pigs and rabbits the serous layer of the stomach and intestines is markedly congested. These effects appear to be the result of self-digestion; they are not present when death is produced shortly after an injection of venom. Rehfuß (*in* Loeb *et al.*, 1913) demonstrated that gastric ulcer could be induced experimentally in guinea pigs by means of subcutaneous injections of the venom of *Heloderma*. Gastric ulcer and hemorrhagic erosions were found in 35 out of 41 (85%) of the animals tested.

Cooke and Loeb could not detect histological changes in animals that died of acute poisoning after a single injection of venom. However, repeated injections over a long period of time led to a slight degree of fibrosis in the liver, kidney, and heart. In the bone marrow the changes observed "probably represent an effort to produce leucocytosis of the polymorphonuclear element." Leopold (*in* Loeb *et al.*, 1913) was unable to detect changes in the spinal cord or myelin of an animal that survived for 13 days after injection of venom. In a rabbit that survived only 75 minutes some changes, includ-

ing disintegration of the Nissl bodies, were detected, and "Chromatolysis was a constant feature in animals living from 48 hours to several days."

Neither the venom of *Heloderma suspectum* nor that of *H. horridum* possesses hemolytic power when added to erythrocytes. However, when lethicin is added to either of the venoms, erythrocytes are hemolyzed. The hemolysins of *Heloderma* venom differ from hemolysins of snake venoms in that they cannot be activated by complements such as those contained in guinea-pig serum. The venom of *Heloderma* is only weakly hemolytic as compared with many snake venoms that have been tested. Also, while many snake venoms contain coagulants or strong anticoagulants, the venom of *Heloderma* exerts only a slight retardation in the coagulation of the blood, according to Cooke and Loeb, who suggest that the results noted may be attributable to the tissue extract rather than to a specific effect of the venom. Van Denburgh and Wight (1900) reported a diaphasic influence on the coagulability of the blood and suggested that thrombosis and embolism might explain the anomalous convulsions occasionally observed in experimental animals. Their observations could not be verified by Cooke and Loeb. Nevertheless Phisalix (1922) accepts the conclusions of Van Denburgh and Wight.

Myers and Tuttle (*in* Loeb *et al.*) report that the injection of the venom into rabbits and dogs produced no marked effect on the number of erythrocytes or the quantity of hemoglobin in the blood.

Secondary effects from the venom of *Heloderma* have sometimes been observed in animals that survived after being bitten or injected. Sumichrast (1880a) mentions the emaciation of a cat that survived the bite of an *escorpión*, and Phisalix (1912a, 1922) reports similar effects in a hedgehog that had been injected with the venom of the Gila monster. Whether such after-effects can result in death several weeks or months after envenomation is problematical. However, Yarrow (1888a) quotes an account concerning a miner bitten on the finger who did not die until "about three months" afterward.

IMMUNIZATION AGAINST THE VENOM

Attempts have been made to immunize animals against the venom of *Heloderma*, although no one has attempted to produce antivenin commercially. Cooke and Loeb experimented with various animals, but were most successful with rabbits. They found that repeated injections of increasingly larger doses of venom produced a resistance to it in these animals. Two of 16 rabbits utilized in experiments eventually were able to withstand about eight times the dose lethal for their controls. Somewhat later Loeb (1921) notes that "while these rabbits were thus to some extent protected against the toxic action of the venom, they did not yield in their blood an antitoxin which was able to protect another individual not immunized previously against the toxic action of the venom." Believing that the venom was "usually not lethal for human beings," Loeb adds that "the production of such an antitoxin is not of any particular practical importance."

Phisalix (1914, 1922) sought to ascertain whether heat attenuates or changes the properties of *Heloderma* venom without destroying its antigenic properties, and whether the injection of cholesterol confers on guinea pigs an immunity to the venom of *Heloderma* comparable to that previously demonstrated for the venom of some vipers. To test the effects of the venom and the drug she used four groups of guinea pigs, each comprised of three animals. Those of the first series received peritoneal injections of 2 milligrams of whole venom; six days later each animal received 3 milligrams, a quantity previously established as the lethal dose for the controls. The animals in the second series received the same dosages at the same intervals, but the solution of venom used had been previously heated under sterile conditions and maintained at a temperature of 80° C. for a period of five minutes. Animals in the third series were injected with similar quantities of venom at the same intervals, but the venom had been boiled for five minutes. Guinea pigs in the fourth series received subcutaneous injections of a saturated solution of cholesterol in ether, 10 milligrams in the first injection, and 15 milligrams in the second injection given six days

later.

Six days after the last injection each of the guinea pigs was tested with an intraperitoneal injection of 5 milligrams of venom, approximately twice the dose necessary to kill an untreated guinea pig. As a result of this injection all animals that had previously received venom that had been boiled or heated to 80° C. died. Those of the second series died in less than two hours, those of the third in four or five hours, with one surviving about 10 hours longer than the controls. In contrast, those that had been injected with cholesterol or with whole venom survived, which indicates that they were immune to almost twice the minimum lethal dose of the controls.

Phisalix offers no theoretical explanation for the results, but it is possible that cholesterol has a precipitating effect on the toxic principles of the venom of *Heloderma* without destroying the antigens. It is now known that cholesterol has antihemolytic as well as antiautolytic qualities that may have been effective in reducing the effects of the venom on the "prepared" guinea pigs. The experiments of Phisalix should be repeated before her conclusions can be considered verified. She does not mention the work of Cooke and Loeb, but in 1922 adds that immunization experiments with the venom of *Heloderma horridum* were carried out by Belden in 1890, whose account she had been unable to procure. Phisalix cites a paper by Belden in her bibliography, apparently intending to designate either one of two articles (Anonymous, 1890a, 1890b), both of which quote letters received from Charles D. Belden, a homeopathic physician living in Phoenix, Arizona. However, Belden's primary interest in the venom of *Heloderma* (*suspectum* rather than "*Heloderma horridus*," the name widely applied by homeopaths to the venom of the Gila monster) lay in his desire to find substances suitable for use as drugs in treating diseases that manifested symptoms similar to those produced by the venom of *Heloderma*. Cooke and Loeb were undoubtedly the first to investigate the possibility of immunizing animals against the venom of *Heloderma*.

EFFECT OF COBRA ANTIVENIN ON THE VENOM

The investigations of snake venoms by Calmette (1907) and others led to the belief that, in general, each antivenin has a specific relationship to the venom that served as an antigen in its production. Calmette, in the light of the information then available, asserted that the neurotoxins of various snake venoms were identical and that an antivenin prepared with cobra venom as the antigen would provide protection against neurotoxins in other snake venoms. Having demonstrated that the venom of *Heloderma* was neurotoxic in its effects, it was of some theoretical interest to Loeb and his coworkers to determine whether cobra antivenin possessed any protecting influence against the venom of the Gila monster.

As the venom of *Heloderma* was believed to be pharmacodynamically similar to, but not so potent as, cobra venom, it was reasoned that cobra antivenin might exert a protecting influence against the venom of the Gila monster. To test this assumption Fleisher and Loeb (*in* Loeb *et al.*, 1913) mixed cobra antivenin with the venom of *Heloderma*, injecting the mixture into mice. The results of their experiments indicate that the cobra antivenin has a "definite though very slight antitoxic effect on heloderma venom; it is able to neutralize a fraction of a lethal dose." In one experiment the antivenin, instead of being mixed with the venom in ad-

vance, was injected at one site and the venom at another. The result was a noticeable delay in the lethal action of the venom, although there was no other evidence of the antivenin's being effective.

Somewhat similar results have been obtained with snake venoms. Schöttler (1951b) reports a slight degree of para-specific action on the venoms of *Ancistrodon*, *Bitis*, *Hemachatus*, and *Vipera* by anti-*Crotalus* and anti-*Bothrops* sera. The neutralizations were far inferior, however, to those produced by specific antivenins. Schöttler questions the utility of antivenins for South American snakes in the treatment of bites from European snakes. As a result of earlier experiments with snake venoms Schöttler (1951a) suggests that the toxic principle of pharmacodynamically similar venoms may be identical, but that the antigenic part of the venom is not toxic.

In view of the distant relationships of cobras and helodermatids, it is remarkable that any neutralization of the venom by cobra antivenin could be demonstrated. The experiments of Fleisher and Loeb do not provide conclusive proof that antigens present in the sera of the snake and the lizard are identical. In fact, larger series of tests and the application of statistical methods would be required to prove that the results obtained by Fleisher and Loeb were not fortuitous.

BITES INFLICTED ON HUMAN BEINGS

IN THEIR NATURAL HABITATS neither the Gila monster nor the *escorpión* is aggressive when encountered. Even though ill equipped for speed, these lizards attempt to escape by retreating or by taking refuge in burrows. But if seized or intercepted in retreat, they are prepared to defend themselves, and the jaws can be brought into play with astonishing agility for animals so slow in their locomotion. The head can rapidly be shifted towards an attacker, despite the limited flexibility of the neck and the relatively short legs. It is impossible, nevertheless, for such lizards to engage their jaws unless an attacker ventures within a few inches. Many venomous snakes strike from a coiled position, launching the head forward with the mouth open and the fangs directed forward, ready to be driven into the flesh of an attacker by a stabbing action. In contrast the Gila monster and its Mexican ally depend entirely on their ability to engage their teeth by means of a simple biting action.

It follows that human beings are rarely bitten unless they have either attempted to capture these venomous lizards or have handled or mal-handled captives. Anonymous (1890a) quotes from a newspaper clipping sent from Arizona by Belden. It credits the original to John A. Spring, a writer of doubtful reliability who asserts that "while prospecting a young miner was bitten just above the shoe." While this is not impossible, it is highly improbable unless the victim carelessly or otherwise stepped on a rather large Gila monster. Even under such conditions it would have been extremely difficult for the lizard to bring its jaws into play.

Goodfellow (quoted by Yarrow, 1888a) writes that he was informed four years prior to his writing that "a man had been bitten on the foot while in the field and died within three hours." Somewhat more convincing is the account of Anonymous (1893), who tells how a Gila monster chanced to crawl over the body of a sleeping hunter, who, "without opening his eyes threw up one hand to dislodge whatever it was" only to have the "teeth of the monster fixed immediately in his naked wrist."

Such encounters with Gila monsters, perhaps erroneously described or exaggerated in the reports, are certainly exceptional. The vast majority of the bites on record have resulted from the careless handling of individuals in confinement. Snedigar (1939) observes that after becoming accustomed to captivity Gila monsters can be handled, even though they should not be treated carelessly or casually. He adds, somewhat caustically, that in the case of the Gila monster, "the familiarity that breeds contempt breeds mostly contempt for the folly of the bitten individual." Relatively few people find it necessary to handle Gila monsters or *escorpiones*. Such lizards are occasionally kept as pets, and owing to their size and gaudy colors and by virtue of their venomous attributes and the resulting notoriety, they have been in considerable demand for display in circuses, sideshows, zoological gardens, and museums. Scientific investigators or collectors also have occasion to handle them. Inevitably there have been victims of their bites, although as will be seen from the case histories, there have been very few casualties.

CASE HISTORIES

While many early accounts of *Heloderma horridum* in México observe that this lizard is regarded as being dangerous, only Dugès (1899) mentions bites actually inflicted on human beings. Natives living within the range of the *escorpión* are almost universally acquainted with its reputation. Consequently they entertain considerable respect for the lizard, which they handle with great care when captured. As most of the lizards supplied to animal dealers have been brought in by natives, it

is probably a safe assumption that on rare occasions the lizard has succeeded in biting a captor. Nevertheless, we have found no published account, other than that of Dugès, of a bite inflicted on a human being by the *escorpión*. Storer (1931) recounts the symptoms resulting from the bite of a "gila monster (*Heloderma* sp.)," so that there is an element of doubt concerning the species in this instance. Other cases on record refer only to *Heloderma suspectum*.

The earliest mention of a human victim ap-

pears to be that of Mr. T. W. Parker of Phoenix, Arizona (quoted by Anonymous, 1879), who says that he is "credibly informed that a man in Arizona, who was bitten while tantalizing a monster, has been paralyzed on that side since." The victim to whom Parker refers may have been the same person mentioned in the account supplied to Yarrow (1888a) by an informant who states that in 1878 or 1880 he saw a Gila monster bite a man by the name of Johnny Bostick, who died within about three months. A second affidavit (in Yarrow, *supra cit.*), signed by R. C. Carlton, who was also present at the time Bostick was bitten, believes that it occurred in 1883.

Yarrow quotes another letter concerning a man by the name of "Yeager" who died after being bitten by a Gila monster in the town of "Fairbanks [now Fairbank] in May, 1885."

Evidently Yeager is the same person referred to in the account quoted by Treadwell (1888) and originally published in a newspaper, the Cochise Record, for May 2, 1884. The clipping states that "Colonel Yeager" lived but a few hours after being bitten. This story has been cited several times since, by Kobelt (1889), Garman (1891), Bradford (1895), and Werner (1913), among others, as well as by Phisalia (1911b, 1922) and Pawlowsky (1927), both of whom credit the account to Lubbock to whom Treadwell sent his letter for presentation to the Zoological Society of London. This is probably the same case discussed by Goodfellow (1907). Many years later an additional account appeared wherein Brennan (1924) refers to the victim as "Col. Yager," stating that he was bitten in Tombstone "in the eighties" and that he died "inside half an hour." There are other discrepancies in the three accounts. The original specifies the "right thumb," Goodfellow says the victim was bitten on the "left thumb and forefinger," and Brennan indicates that it was "the finger."

Regardless of the details, it is plain, despite the inaccuracies of the three accounts, that Yeager, Yearger, or Yager died shortly after being bitten. These published records, supplemented by the account of Anonymous (1893), had appeared before Loeb (*in* Loeb *et al.*, 1913) stated that "No death of a human being has come to our knowledge that can be attributed to the bite of a gila monster." Loeb's

comment was quoted by Storer (1931) and by Vorhies (1917), who adds that a reputable physician of Tucson "made considerable effort to authenticate a single case of death caused by a Gila Monster, and has failed to do so." Later Vorhies (1936) modified his views, writing that "in twenty years of experience in Arizona, following up reported cases of bites, no death resulting primarily and unquestionably from such a bite has occurred." He adds a footnote, however: "Only two near-authentic cases are known to the writer, both of which involved some alcoholism." Loeb (1921) was somewhat less dogmatic in a later statement wherein he observes that "It is said that in some instances persons have died as a result of a bite. However that may be, we have not been able to find an authentic case where death was due to the action of the *Heloderma* venom." Andrews (1937) says "there are no authentic cases where death resulted," probably having gotten this information from Loeb.

Gadow (1901) says a few cases of death are on record, but Pauloff (1926) asserts that the bite is very painful but not fatal to man. Berridge (1926) comes to quite different conclusions, but cites no sources. He says that "several instances have been recorded of human beings being killed as the result of the bite from one of these reptiles [Gila monsters]." Arrington (1930) more cautiously states that "there appears to be no authentic case of a death caused directly and solely from the bite of a Gila Monster" but pointedly comments that "science invariably gives a weakened heart or a nervous system as the real cause when death comes soon after a bite, although from time to time reports come to hand that tend to make the public wonder if this viewpoint is entirely correct. A recent case [presumably that reported in the Arizona Republic for April 29, 1930] in a town near the writer's home was handled by a competent physician, and yet the patient died within three hours after the attack." Dunn (1951) more recently writes that "there have been human deaths following bites from Gila monsters, but even the best reported case (death in less than an hour) leaves room for some doubt as to the venom's being the sole or even the main cause of death." Shannon (1953b) concludes a summary of two case histories with the comment that "a prolonged bite from a

large Gila monster on a small person could produce extremely grave symptoms, even though most of the deaths recorded in the literature may be discounted."

Several published accounts (Storer, 1931; Arrington, 1930; Woodson, 1943a, 1943b, 1947, 1950) briefly discuss one or more individual cases of bites by Gila monsters, but only Woodson has attempted to summarize the results of a more extensive survey. He (Woodson, 1943a, 1943b, paraphrased by Hylander, 1954), states that after "a search of medical journals, scientific reports, popular magazines and books" totaling over 300 references between 1882 and 1939, he uncovered 47 case histories, 15 of which ended in death. However, only one case "was thoroughly investigated, and it was noted that the victim previously had had a weak heart and drank to excess."

Four years after his earlier surveys were published Woodson (1947) reports that 29 out of 136 cases ended in the death of the victims. Stebbins (1954) mentions the same figures, but says that "29 reputedly ended in death." By 1950, however, Woodson had revised his figures upward, stating that he had assembled reports of 158 cases, inexplicably with fewer deaths, for only 23 of the 158 were reported to have died. Like previous authors, Woodson felt impelled to add that of the 23 that allegedly died from the bites, "some were chronic alcoholics, others had various diseases, while insufficient data had been obtained on the remainder to form an opinion." In his other articles, most of them written for non-technical publications, Woodson discusses the problems involved in obtaining satisfactory data. Following the statistics supplied in 1947 Woodson observes: "The probability that much of the details of the fatal cases are erroneous or entirely fictitious can be illustrated by a contemporary case. The author in his correspondence has received six letters that refer to the [same] victim. One writer tells of the bite and, in conservative details, charts the symptom picture, whereas another explains that it took place on the nose and disfigured the man for life. The remaining four ranged between these extremes.

"To learn the truth the author sent a questionnaire to the man, himself. His reply most certainly vouched that his reported symptoms were greatly exaggerated. 'My Gila monster

bites were of little consequence,' he writes. 'None of the bites were serious.'"

Aside from inaccuracies resulting from faulty memories or from exaggerations presumably inspired by the desire of some informants to provide a detailed or more colorful story, there is the additional problem of determining whether different accounts refer to the same victim or to other individuals. The person bitten may not be indicated by name or, what is even worse, an incorrect name may be used. It cannot be ascertained from Woodson's figures concerning mortality rates whether separate accounts of the death of one individual have been counted as additional fatalities, or whether he sought to identify the victims. At least nine authors have mentioned the fatality first reported in the Cochise Record, and an uncritical compilation of cases could easily indicate nine deaths where only one actually occurred.

In listing the accounts of individual bites, therefore, we have sometimes included under a single heading several accounts that refer to the same victim. Information has been obtained from diverse sources, including scientific journals, magazines, and correspondence. The list has manifest shortcomings, but without better sources of information there is no alternative. Inadequate as many statements are, they provide some clues to symptoms and the circumstances under which bites most often occur. Any bite mentioned, however minor, has been included. Insofar as possible, accounts are listed in chronological order, quoted verbatim, with their sources indicated.

CASE No. 1

"Mr. Parker does not think the monster able to defend itself with its teeth, the latter being so small. Yet he says that he is credibly informed that a man in Arizona, who was bitten while tantalizing a monster, has been paralyzed on that side ever since" (Anonymous, 1879).

As suggested above, this is quite possibly the same case referred to by Yarrow (1888a), who quotes two accounts. The first was secured from Dr. S. Guiberson of Ventura County, California, who provided the following affidavit:

"G. J. Hayes, a miner in from the Frazer mine, says that in 1878, or '80, in Tip-Top Mining Camp, Arizona, he saw a Gila monster

bite a man by the name of Johnny Bostick, who at the time was under the influence of liquor. That he took hold of the *Heloderma* and shoved his finger at it, and the reptile seized his finger, and its jaws had to be pried open before he could disengage his finger. The *Heloderma* was 22 in. long and lay on the card table. It was also seen by a man named Lou Smith, and a lot of Italian miners. Immediately Mr. John Bostick drank large quantities of liquor, and from the effects of the bite one side was paralyzed, and he died in about three months, April 19, 1878. I hereby certify that the above statement is correct. (Signed) G. J. Hayes. Subscribed and sworn to before me, a notary public, this 19th day of April, 1886. S. P. Guiberson."

Yarrow prefaces the second account with the comment that "it differs somewhat from the first, but relates to the same individual. The query is, was the *Heloderma* bite the cause of death or was it the whiskey so lavishly administered."

"State of California, County of Ventura.—R. C. Carleton who first being duly sworn, deposes and says that he was present at the time and knows of his own knowledge that Johnny Bostick, of the Tip-Top, Arizona, was bitten by a Gila monster, from the effects of which he afterwards died. That the Gila monster seized one of the fingers or thumb of the said Johnny Bostick, and that in order to disengage the reptile the boys cut its head off, that deponent thinks it occurred in 1883. Subscribed and sworn to before me this first day of December, 1886.—R. C. Carleton."

CASE No. 2

"In removing them from cage to cage, or handling them [Gila monsters] for other purposes, the utmost care has usually to be exercised, due to their doubtful reputation and not over gentle appearance [what bearing their appearance had on the care exercised is not clear]. Mr. Henry Horan, the superintendent of the National Museum, received on several occasions slight bites from these specimens, but the wounds were never followed by any untoward symptoms" (Shufeldt, 1882).

CASE No. 3

"On the 18th Inst., in the company of Pro-

fessor Gill of the Institution, I examined for the first time Dr. Burr's specimen [a Gila monster that had been in captivity for nearly six months before being shipped to the Smithsonian Institution] then in a cage in the herpetological room. It was in capital health, and at first I handled it with great care, holding it in my left hand examining special parts with my right. At the close of this examination I was about to return the fellow to his temporary quarters, when my left hand slipped slightly, and the now highly indignant and irritated *Heloderma* made a dart forward and seized my right thumb in his mouth, inflicting a severe lacerated wound, sinking the teeth in his upper maxilla to the very bone. He loosed his hold immediately and I replaced him in his cage, with far greater haste, perhaps, than I removed him from it.

"By suction with my mouth, I drew not a little blood from the wound, but the bleeding soon ceased entirely, to be followed in a few moments by very severe shooting pains up my arm and down the corresponding side. The severity of these pains was so unexpected that added to the nervous shock already experienced, no doubt, and a rapid swelling of the parts that now set in, caused me to become so faint as to fall, and Dr. Gill's study was reached with no little difficulty. The action of the skin was greatly increased and the perspiration flowed profusely. A small quantity of whisky was administered. This is about a fair statement of the immediate symptoms; the same night the pain allowed of no rest, although the hand was kept in ice and laudanum, but the swelling was confined to this member alone, not passing beyond the wrist. Next morning this was considerably reduced, and further reduction was assisted by the use of a lead water wash.

"In a few days the wound healed kindly, and in all probability will leave no scar; all other symptoms subsided without treatment, beyond the wearing for about forty-eight hours, so much of a kid glove as covered the parts involved.

"Taking everything into consideration, we must believe the bite of *Heloderma suspectum* to be a harmless one beyond the ordinary symptoms that usually follow the bite of an irritated animal. I have seen, as perhaps all surgeons

have, the most serious consequences follow the bite inflicted by an angry man, and several years ago the writer had his hand confined in a sling for many weeks from such a wound administered by the teeth of a common cat, the even tenor of whose life had been suddenly interrupted" (Shufeldt, 1882).

Nearly two decades later Shufeldt (1901) redescribed the accident, adding details that must be considered more imaginative than accurate. The Gila monster that inflicted the bite is now described as having "a length something like twenty inches." Shufeldt continues, "The small eyes had a wicked look, and glared an emerald green as I handled the fellow over and over to examine his points, as any naturalist would. Being satisfied with my investigation, I was about to return him to confinement, when all of a sudden, by a quick movement of which I hardly expected this great, sluggish reptile could be capable, he turned and seized my thumb in his mouth, and with his sharp, glistening teeth ripped the flesh to the bone. At the time his clear, transparent saliva was drooling in plenty from the angles of his ugly jaws, and his victim doubtless received the full benefit of it.

"I was taken home in great pain in a carriage by Dr. Emil Bessels, of the Polaris expedition, the hand and wrist swelling to no small degree in the meantime. However, I recovered from the inflicted bite under very simple treatment, and have never felt any injurious after-effects from it since. This bite had a peculiar influence over me, and was to a large degree instrumental in inciting an impulse to make a complete study of the life history of the *Heloderma*, and this was inaugurated by my publishing in a natural history journal, to start with, an account of the bite I had received."

Van Denburgh (1898) after raising the question of why no serious symptoms have ensued in some instances, comments, "Several reasons must, I think, have suggested themselves. Dr. Shufeldt, it will be remembered was severely bitten on the thumb, and concluded that the bite of the gila monster is no more poisonous than that of other angry animals; for example a cat. But Dr. Shufeldt expressly states that the wound was made by the upper teeth penetrating to the bone . . . the saliva of the upper jaw is harmless at all times, the

venom being confined to the lower jaw. So it may well be that Dr. Shufeldt owes his life to the circumstance that the injury to his thumb was inflicted by the upper instead of the lower teeth of the monster."

CASE No. 4

No other case has been described so many times or quite so widely cited as that of "Colonel Yeager," whose death was reported in the Cochise Record for May 2, 1884. Discrepancies in the various accounts have been pointed out above to exemplify the sort of inaccuracies that are perpetrated by well-meaning but incautious reporters. As can be seen from the following accounts, much that has been written is clearly supposition, with the imagination substituting for memory, especially when the lapse of time made recollection more difficult.

The original newspaper account quoted verbatim by Treadwell (1888) is probably more accurate than any that followed it. Additional details and interpretations published later are probably less reliable. Treadwell supplies the following extracts from the Cochise Record:

"Sunday evening Dr. Matthews was summoned, by telegram to Fairbanks (a railway-station near Tombstone, Arizona Territory, U.S.A.), to attend Colonel Yeager, who was reported seriously ill. Owing to a delay in the telegram the doctor did not reach the patient until several hours after his death, which had been very sudden.

"It appears that Yeager had been fooling with a Gila Monster, and in attempting to open the creature's mouth, was bitten on the right thumb. Instantly the poison took effect, and although every convenient remedy was applied, he lived but a few hours. An inquest was subsequently held, and a verdict returned in accordance with the above facts.

"As this is the third or fourth death which has occurred in the Territory from bites of this reptile, it should set at rest, at once and for ever, the theory so prevalent that their bite is not poisonous."

The account obtained by Yarrow (1888a) from Dr. F. V. Ainsworth, was supplied by Dr. G. E. Goodfellow, who evidently obtained his information from witnesses, but not necessarily at the time the bite occurred, for his letter was written July 23, 1887, over three years

later. Goodfellow writes:

"The Fairbanks case was as follows: Yeager, about 55 years of age was in May, 1885, in Fairbanks, Arizona Territory, bitten by a Gila monster. He, to prove the innocuousness of the beast, put his left thumb and forefinger into its mouth, and he was bitten. He was immediately loaded to the guards with whiskey—it happened in a saloon—and he seemed all right, save for a slight numbness and swelling in the hand and arm. He sat down in a chair in the saloon, talked with those around for an hour. The crowd thinning out, he seemed to drop asleep. In about an hour more, the saloon keeper spoke to him, but not making a reply, he was taken hold of and found to be dead. I was sent for, but before I could leave received a second message announcing his death. He was a man addicted to the use of liquor, and so far as I can ascertain had been on a prolonged spree for months. Whether he died of the reptilian poison or a combination of whiskey, disease and Gila monster I cannot say.

"That the Gila monster is a poisonous lizard cannot now be denied. That its bite is fatal uniformly is open to discussion. I have always considered that they were a trifle more poisonous than the scorpion, tarantula and centipede, not even approaching the rattlesnake, and I have been accustomed to regard the bite of the three first mentioned as little worse than the sting of a bee or wasp. I have known of bee stings killing, but though I have seen many bitten, and have had a personal experience as well, never have I known of a death to occur from the bite of a scorpion, tarantula or centipede. That they can kill under certain conditions I am convinced."

By 1907 the story of Yeager's death had probably been told and retold in Arizona, with names and dates sometimes substituted, or possibly with elements of other stories incorporated. It is far from certain whether the statement credited to Mr. W. C. Barnes of Las Vegas, New Mexico, by Anonymous (1907) can be identified with the Yeager story, but evidently Goodfellow (1907) believes it to be, as can be inferred from his comments. Barnes is quoted as knowing of two bites inflicted by Gila monsters, from one of which the victim died. Barnes writes, "The first man was in Tombstone, Ariz. The Gila was tied by the leg

in a saloon as a curio, and a drunken gambler named Brown was teasing it. He carelessly stuck his first two fingers into its mouth, which immediately closed down on them, and could not be released until the reptile's head was cut off and the jaws cut apart. Brown suffered horrible agony for almost two days, and in spite of all efforts he died."

To this Goodfellow replied: "Being perfectly familiar with the entire history of the cases cited as evidence of the poisonous characteristics of the reptile, I write to correct the narrator in a few minor details as well as to discuss the venomous nature of the bite.

"The first case mentioned did not occur in Tombstone, Ariz., but in either Fairbanks or Contention (two small towns then existing about ten miles from Tombstone), the former I think. The man was bitten and died, and I was one of the physicians summoned to attend him. The autopsy demonstrated cirrhosis of the liver, ascites, fatty heart, etc., and his history evidenced the cause of his death to be due to acute alcoholic poisoning grafted on chronic alcoholism."

It is not a little amazing to find that 20 years after Yeager's death, Goodfellow is able to supply post-mortem evidence omitted from the account he supplied to Dr. Ainsworth less than four years after the victim was bitten. An additional account, that of Brennan (1924), while incorrect in detail, preserves the more important facts with as much accuracy as can be expected after a lapse of half a century. Brennan writes, "I have in my school museum a stuffed Gila monster, *Heloderma suspectum*, that actually killed a man at Tombstone, Ariz. in the eighties. My uncle, Judge Alexander Freeman, who lived in Tombstone for many years and helped clean out the thugs who gave it that frigid name, sent me this reptile and gave its history.

"It had been tied to a stake in front of a hotel, and a man, Col. Yager, was teasing it by poking his finger at it. It made a sudden spring at him, seized him by the finger, and began to chew. It was finally pried off and killed. The colonel died inside of half an hour."

Other references to the death of Colonel Yeager (Kobelt, 1889; Garman, 1891; Belden, in Anonymous, 1890b; Bradford, 1895; Werner, 1913; Pawlowsky, 1927), credited either to Treadwell or Lubbock, merely cite the original as copied in the Proceedings of the Zoological

Society of London. Phisalix (1911b, 1922) supplies a brief summary, and complains that the author gives no details of the symptoms or of the remedies applied in an effort to save the victim.

CASE No. 5

The following is of doubtful value, as the writer, Dr. G. E. Goodfellow (quoted in Yarrow, 1888a), notes: "About four years ago on the lower San Pedro [River, in southeastern Arizona] I was informed that a man had been bitten on the foot while in the field and died within three hours. I could neither prove nor disprove the case." Such an accident might conceivably occur if the man was without shoes, as a native of the region might have been in 1884.

CASE No. 6

Like the case of Colonel Yearger cited above, that of Walter L. Vail has been the subject of controversy. The earliest account of the case probably appeared in the Daily Citizen published in Tucson, Arizona. Anonymous (1890a) quotes a story that appeared in the same newspaper under the date May 15, 1890. This contains only an incidental reference to the case, "In view of the accident which happened a few days ago to Hon. Walter L. Vail." But additional information was later supplied by Belden (quoted by Anonymous, 1890b) who writes, "Mr. Vail, of Tucson, whose case was reported ["mentioned" would have been more apt] in the Recorder, has recovered from the bite he received about three months ago. The only perceptible result has been a swollen tongue, which seems unwilling to resume its former proportions. The treatment in his case was that so strongly recommended by European authority: profuse sweating by administration of Jaborandi [an extract from the leaves of *Pilocarpus microphyllus*, a remedy advocated several years earlier for the treatment of snake bite; Yarrow (1889) carried out experiments with rabbits, reporting that it appeared to have "some antidotal effects," but "in fowls it fails"]. Mr. Vail says that his suffering was intense, the pain proceeding from the wounded part toward the head and back. Immediately after receiving the wound, which was upon his index finger both the wrist and the finger was [*sic*] tightly bandaged. Medical assistance was not secured for

two hours. Then the wound was cleansed and dressed and bandages reapplied. It was found that for three days those intense pains would shoot toward the head and spine upon giving any relief to the bandages."

Belden adds that "it is generally understood that a victim who is pretty well 'pickled' with bad rum will certainly die from the bite. Mr. Vail's case is a negative instance in favor of the theory. He was a man of temperate habits. An affirmative instance is that of a miner [Johnny Bostick, the miner of Case No. 1?], living not far from here, who is supposed to have died a short time ago from the effects of a bite, after having laid in a lingering death-like state for several months. He was bitten while drunk. It appears that man does not die so quickly from the effects of this poison as other animals do, but that all cases well authenticated show a long, lingering, wasting sickness."

Barnes (quoted by Anonymous, 1907) states, "The second case was in the fall of 1889. Walter Vail started from the 'Empire' ranch, near Benson, Ariz., to ride into town on horseback, some fifteen miles. A short distance from the ranch a monster was sluggishly dragging its way across the road. Thinking to take it in for a friend, he got down and killed it—or at least he thought he killed it. To carry it easily, he tied it on his saddle behind him, using his saddle strings for the purpose. As he loped along he thought to assure himself it hadn't dropped off by reaching around behind him with his right hand and feeling for the monster.

"It was there, and not nearly as dead as he thought. His first finger went into the reptile's mouth clear to the knuckle, and instantly those jaws with the long, sharp, daggerlike teeth closed on Vail's finger. With his left hand he managed to get his knife out and cut the saddle strings, and then had to dissect the head and jaws to get his finger from their grip.

"Vail then spurred his horse into Benson and found an engine in the yards. A hasty exchange of telegrams with the division superintendent and Tucson took place and in a few minutes he was on the engine and racing over the road for Tucson, where an eminent surgeon resided at that time. Vail lay at death's door for two months and that finger today is useless and shriveled up from the effect of the bite."

Goodfellow (1907) replied to Barnes as

follows:

"In the second case, that of Mr. Vail, the circumstances surrounding the accident were as related. Mr. Vail, believing as did most of us at that time that the lizard was a venomous reptile, followed the usual frontier methods of treatment—ligation of the finger, with large quantities of alcohol internally; and his physician, Dr. Handy, after his arrival cauterized the wound, making an excessively sore finger for some time, but the finger neither was paralyzed nor withered nor useless afterward; and just prior to his death, which occurred a few weeks ago as the result of a street-car accident in Los Angeles, he had as free use of the finger as he ever had, and I saw him the day preceding his accident." Woodson (1943b) mentions the same incident apparently when he refers to a "cattleman who caught a Gila monster [and] tied it onto the back of his saddle."

Discussion of Vail's bite was revived by Woodson (1950), who asserts that "The victim of Arizona's most famous Gila monster bite was Walter L. Vail, owner of the Empire ranch just southeast of Tucson. Although it occurred in May of 1890, it is still talked about. Some say he died; others, that he recovered but that each year at the date of the bite he would turn black and blue. Even in Sonora, the Mexicans have the story of the cowboy who rode into camp—dead—after being bitten by a Gila monster."

Woodson continues "None of these tales is true. I got the real facts from the Arizona Pioneer Historical Society, University of Arizona, Tucson. Its curator, Carl F. Miller, permitted me to copy a letter dated March 24, 1928, written by Walter's brother, Ed. L. Vail, at the request of Major George H. Kelley, state historian at that time.

"Here's what actually happened. While attending a spring roundup, Walter Vail killed a large Gila Monster, which he tied on the back of his saddle. He rode back to the roundup camp. There, he found his saddle loose. To get off his horse, he put his hand up on the cantle. The Gila monster—not dead as thought—seized the middle finger of his right hand and hung on like a bulldog. Bob Robinson, who was with him, pried its mouth open.

"Subsequently, they reached Dr. J. C. Handy, who treated the wound. Most noticeable symp-

toms were a swollen tongue and impairment of the glands of the throat. 'My brother apparently recovered,' wrote Ed, 'but his throat was affected sometime after.' This clears up the 'ridiculous stories published about this incident,' as Ed phrased it."

The conflict in these four accounts can be attributed in part to the desire of each informant to make his story sound the more authentic by supplying details, some of which may, of course, have been modified or revised to suit the tastes of the narrators.

CASE No. 7

Having given his version of the death of Colonel Yeager and the treatment administered to Mr. Vail, Goodfellow (1907) proceeds to relate how he himself was bitten.

"In December, 1891, the writer, who was then engaged in studying the Gila monster and other alleged venomous reptiles and insects, had in his collection a dozen or more 'monsters,' and while handling one of them was seized by the left index finger just back of the nail, and a severe bite inflicted. No crowbar, knife, or hatchet was required to disengage the enraged animal, which hung on viciously; merely a strong pull with pressure of the jaws liberated the digit, which was treated simply, and aside from the usual soreness accompanying a lacerated wound of the pulp of the finger involving the nail, no inconvenience was experienced, nor was the writer prevented from following his usual professional work, except—naturally—the surgical side of it. No constitutional symptoms whatever supervened. At that time, owing to the investigations which he had been making for some months, he had arrived at the conclusion that the belief in the poisonous nature of the lizard was purely mythical and superstitious, the remnant of primeval man's antagonism to all creeping things.

"In addition to the three cases mentioned, I have known quite a number of people who have been bitten by the lizard either on the foot or the hand, but in no instance has death been the result. If the usual folk treatment of ligation of the wounded part with alcohol internally was followed by cauterization of the wound, general *malaise* with a more or less sore member has succeeded, but not death.

"The Gila monster, of which there are two

species on the deserts of the Southwest, has neither poison glands nor fangs. Its teeth (?) are not hollow, consequently nowhere within the jurisdiction of its mouth is there the wherewithal to envenom a wound made by them, and this assertion is based upon numerous dissections and anatomical investigations. If much irritated it does eject the contents of its stomach, which are more or less fetid, while hanging to an object it has been exasperated into biting. This may or may not be accidental, for it does not always occur; only after swinging or shaking severely the reptile while still attached to the object bitten. That neither knife, chisel, hatchet, nor crowbar is needed to release an object from the grip of its jaws, simple inspection of the anatomical structure of its head will suffice to demonstrate. This grip is a firm one, but one released by an unterrified person with comparative ease.

"About this same time (1891) exhaustive studies were made by some of the attaches of the Smithsonian Institution, among whom was Dr. R. W. Shufeldt, concerning the nature of the animal, and conclusions reached which the writer had previously attained—that the reptile was non-venomous; and it may be accepted as conclusively demonstrated that the bite of the 'monster' is innocuous *per se*."

Goodfellow apparently had reversed the stand he had taken 20 years previously when (quoted by Yarrow, 1888a) he had stated that it could no longer be denied that the Gila monster was a poisonous lizard. At the time of his second writing he was living in San Francisco, where another physician, Dr. John Van Denburgh (1898), had carried out experiments that proved beyond doubt that the Gila monster produced a toxic saliva. But Goodfellow seems to be unaware of any investigation subsequent to 1891. He seems moreover to have forgotten that Shufeldt (1890) described the venom glands, even though he was in error in his assertion that the ducts passed through the ramus of the lower jaw, as Shufeldt admitted in 1891. Goodfellow could scarcely have made the dissections he mentions without having seen the fangs or the venom glands, the existence of which he denies. In view of such assertions and the lack of any likelihood of a person's being bitten on the foot, it is difficult to accept his statement that he knew a number of people

bitten by the lizard "either on the foot or the hand." It would seem that Goodfellow was even more careless in his statements than he was with his Gila monsters.

CASE No. 8

Anonymous (1890b) quotes from the May 15, 1890, issue of the Daily Citizen of Tucson, Arizona, "an extract of a paper written by our townsman, John A. Spring," said to have been published the previous month in a British magazine, Chambers' Journal. Spring, who was both gullible and prone to overstatement, was a source of considerable misinformation concerning Gila monsters in the last decade of the nineteenth century. This may be inferred from Garman's (1891) and Werner's (1913) quotations from his writings (see also the section of the present paper dealing with folklore). Perhaps Spring's account, which follows, should not be taken too seriously.

"A young miner while prospecting was bitten just above the shoe. Although previously in the best of health, he at once began to lose flesh, became melancholy, and died in a few months in the manner of those who succumb to what in Germany is called the galloping consumption."

CASE No. 9

Also from a newspaper clipping quoted by Anonymous (1890a) is the report of a conversation supposedly overheard by a newspaper reporter. Portions of the story sound plausible, though it is seriously to be doubted whether death occurred so soon after the bite. The unidentified speaker, discussing Gila monsters, is quoted as saying, "A friend of mine had one in a box just outside a saloon, and one day a chap came along who was so drunk he was ready to eat up the earth. He was afraid of nothing, and when he saw the box and the sign 'Hands Off—Poisonous,' he swore he could handle it, and before anyone could prevent him, he ripped off the slats and made a grab for it. The thing twisted around and bit him on the finger, and, to make a long story short, I saw him die in the middle of the street a short time after."

CASE No. 10

Phisalix (1922) in her bibliography credits

the following story to Garman, who may have called it to her attention. Actually it first appeared in the Philadelphia Times. It was quoted without comment by Anonymous (1893), who indicates the original source. It is dated June 22 [1893?], presumably having been written by the Philadelphia Times correspondent at Florence, Arizona. The journalist may have supplied some fanciful details, including the discovery of "six newly born young" in the cave where the victim was allegedly bitten. The lurid story of the bite and its consequences is recounted as follows:

"Richard M. Farthingay, a tourist from Minneapolis, returned here last evening with the remains of Arthur James, who had accompanied him on the journey, and who had died the day before from the bite of a Gila monster.

"The story as related by Mr. Farthingay, who seems to be utterly prostrated by the horror of the occurrence, is indeed a terrible one. It appears that following a blacktailed deer the two hunters found themselves near a small water course emptying itself into the Gila, and at last struck camp for the night on this creek. The weather proving rainy they sought shelter in a little cavern formed by a heap of rocks, taking the precaution to close its entrance with coals from their camp fire, for fear of rattlesnakes, but not observing the foe within.

"Just at daylight Mr. Farthingay was awakened by something that had just slidden over his prostrate body and fallen to the floor of the cavern. Opening his eyes he saw the reptile-like shape and snake head of one of these venomous creatures. It was traveling rapidly, and before Mr. Farthingay could reach his gun had encountered the sleeping form of Mr. James, whose breast it attempted to climb.

"Disturbed by the touch of the animal, the unfortunate man, without opening his eyes, threw up one hand to dislodge whatever it was, and catching it by the tail would have thrown it from him, but the deadly teeth of the monster fixed immediately in his naked wrist, and though Mr. Farthingay hastened at once to his friend's relief and endeavored to pull it off, it held on like the grim death it was. Then, though fearing to strike the man instead of the reptile, he seized his gun and fired the contents into the creature's body. The monster let go its grip on Mr. James and made an effort to reach this

new antagonist, but a second volley tore its head from its body.

"Mr. Farthingay now turned his attention to his friend, and found that he had fainted. On being restored to consciousness Mr. James complained greatly of his wrist, which he said felt as if on fire, and which almost immediately began to swell. Immoderate thirst now set up and fever ensued, so becoming very much alarmed about his companion, Mr. Farthingay proposed setting off at once to town to procure medical attention for the wound, but Mr. James, fearing to die alone, implored his friend not to leave him. In answer to his prayer, the other agreed to await the course of the trouble, and fetching water from the creek bathed the wounded arm, but in less than half an hour the entire member was swollen to nearly three times its natural size, and from some slight discoloration assumed a deep purplish hue, nearly black, in splotches about the larger blood vessels.

"Delirium now set in, and while anxious to summon assistance Mr. Farthingay was forced to remain to restrain the now raving, shrieking man, who again and again attempted to throttle his companion when the latter endeavored to keep him from running out of the cavern to the creek. At last, worried out, Mr. Farthingay was flung aside by the frantic sufferer, who broke out of his grasp and ran to the stream howling. The other followed as rapidly as possible, but only arrived in time to see Mr. James struggle down the shelving bank, then totter forward and fall.

"When he reached him it was to find life entirely extinct, James lying with his head in the water and his own teeth fixed in the swollen, gangrened arm. After exhausting such restoratives as he had with him, Farthingay dragged the body back to the cavern, when he set off to seek assistance. A few miles further on he came across an old Mexican who living near the river in an adobe hut was also the fortunate and opulent possessor of a donkey and cart. With these latter the two men returned to the cavern, when James' body was placed on the cart and driven to town. Before leaving the place, however, Farthingay made a thorough search of the cavern and discovering a female monster with six newly-born young ones, killed the entire lot. The mother, though shot nearly to pieces, made an assault on the hunter, but his

heavy hunting boots prevented her from biting him. The old Mexican who accompanied Farthingay and his friend's rapidly decaying body to town declared that James was the fourth man who has been killed by these deadly creatures on the river this spring. There is no known antidote for their poison."

CASE No. 11

As reported by Anonymous (1889) in the Medical News, "A snake charmer at Coney Island not long ago was bitten on the hand by a Gila monster. The bite of the creature is sometimes fatal and always serious. The immediate application of a tight bandage around the wrist prevented the absorption of the poison into the general circulation while suction by the patient himself, and free bleeding, aided in getting rid of it. The patient recovered without any serious symptoms and without sequelae."

CASE No. 12

Dugès (1899) states that Brehm (in the "Merveilles de la Nature," which we have not been able to locate) tells how in Mexico Börsch irritated an *escorpión* that bit his finger as well as that of a friend. Although the wounds bled and were very painful, they healed rapidly. This is the only account we have discovered that mentions a bite inflicted by *Heloderma horridum*. Dugès adds that "M. Word [Ward?]" of Rochester in the United States has told him that his children, while playing with *Heloderma suspectum*, were bitten without any unfortunate consequences.

CASE No. 13

Snow (1906) provides the following description of his encounter with a Gila monster in Arizona: "During the past summer, on July 26, 1906, I had the fortune to be bitten on the ball of the right thumb by a Gila monster, one of a pair which had been captured some two weeks previously and kept in a large box awaiting our departure from camp upon our homeward journey. In the same box were also placed two specimens of a very large frog. Late one afternoon it was observed that one of the frogs had been bitten by one of the Gila monsters. The next morning the bitten frog was dead and its body had shrunk to half its former dimensions. This was the first indication I had ob-

served suggesting that the *Heloderma* might be venomous.

"When we broke camp the two Gila monsters were placed in a galvanized-iron water-bucket, over the top of which a towel was tied to prevent the escape of the reptiles. I sat upon the seat with the driver with this bucket in front of me between my feet. The motion of the wagon apparently disturbing the serenity of the reptiles, they soon began to attempt an escape by pushing their heads against the towel. Being fearful that they would accomplish their purpose, whenever the prominence caused by the upward pressure indicated the location of the head of one of the monsters, I would force it down by a rap with the handle of the driver's whip, or with my spectacle case. At last, becoming a little careless, I used my hand instead of the artificial tools. In one of these careless movements I was struck in the ball of the right thumb by one of the indignant reptiles, receiving six incisions, four of which were of considerable depth, from which blood flowed in considerable quantities. Fortunately the jaws did not close upon the thumb so that there was no crushing effect produced. I sucked the blood from the wounds until one of my associates, Mr. L. A. Adams, who had some years ago suffered severely from a rattlesnake bite, provided me with a vial of permanganate of potash, which was kept in contact with the wounds for about an hour. No evidence whatever of poisonous effect from this bite was to be detected, and I began to doubt the venomous character of the reptiles, since, notwithstanding the prompt application of the proper remedies, it seemed inevitable that at least some faint trace of the poison should have been left. But unless the Gila monster were in fact a venomous reptile, how could its universal bad reputation be accounted for? I think I may say that, without a single exception, the residents of Arizona and Sonora believe the bite of the *Heloderma* to be a very dangerous infliction, and several instances were circumstantially related to me of ranchmen and cowboys who had suffered untold agonies and had narrowly escaped death after one of its vicious attacks."

CASE No. 14

A bite inflicted by a Gila monster in Brooklyn is briefly described by Englehardt (1914) seven

years after its occurrence: "On October 26, 1907, a museum attendant was bitten on the fleshy part of the base of the thumb on the right hand. The reptile's hold was extremely tenacious, and some time, perhaps a minute, elapsed before the hand was released. The wound showed six small punctures. Swelling and discoloration of the hand, accompanied by great pain in the hand and arm, followed quickly. Although immediately placed under medical care, when the patient reported for duty two weeks later, he still complained of numbness in the hand and arm and occasional dizziness. Lack of mental reserve and a physical condition below the average in this case no doubt contributed in rendering the effect of the Gila Monster's bite unusually severe."

CASE NO. 15

No details are provided, but Werner (1913) concludes his account of a Gila monster's behavior in captivity by stating "Because of its unpleasant smell and a malicious disposition (when disturbed it suddenly became angry and snapped wildly at the intruder, with the venom dripping from its mouth), which was expressed in biting his keeper on the finger, it was sent to the zoological garden in Frankfurt am Main [translation from the German]."

CASE NO. 16

Few individuals have been better qualified than Phisalix to describe the effects of the venom of *Heloderma*. Her account of a bite inflicted by a captive Gila monster contains one of the more reliable descriptions of the symptoms experienced, although, as noted above, her conclusion concerning the small amount of venom that might prove fatal to a human being is open to question. Phisalix' account originally appeared in 1911 (1911b), prefaced by a review of the literature and a quotation from the account of the death of Colonel Yeager, which mentions, but does not describe, other mortalities from *Heloderma*. In 1922 Phisalix repeats her earlier description and review, but adds a quotation from Shufeldt's account of the bite inflicted on him in 1882. She evidently believed that the bite she received was of a more serious nature than the one received by Shufeldt. The following is a translation of Phisalix' account as republished in 1922:

"Between these two sorts of cases, the mortal ones [including that of Colonel Yeager] confirmed by several witnesses, and the other mild ones, like that of Shufeldt, stands the one I have observed on myself, and in which nervous shock did not play a role.

"On June 6, 1911, at about 5 o'clock in the afternoon, I was examining one of the beautiful specimens of the Reptile Menagerie and, holding the animal with the left hand, was trying with the right index finger to pull down the lower lip to see the grooved teeth and the openings of the excretory ducts of the gland. The examination had been terminated to our satisfaction when, by a sudden lateral movement, quite probably reflex, of the head, the Gila monster seized the end of the right index finger lengthwise between the right half of its jaws.

"The constriction was so strong proportionately to the size of the animal (which measured only 40 cm. in total length and weighed just 520 gr.), that I could not have hoped to free myself alone, without choking the animal. But fortunately, Dr. Deyrolle, who happened to be present, came to my aid with instruments which he luckily had at hand: with the help of an oyster knife which he used, like a screw-driver, in the space that remained to the left with the finger pushed to the right, he succeeded very adroitly in opening the jaws of the *Heloderma* without doing any harm to it, and in freeing me. We were then able to replace the Gila monster safe and sound in its cage where it reverted to its torpid behavior and usual calmness, without showing any sign of irritation. The instillation of the venom had lasted several minutes.

"Only one of the venomous teeth had penetrated deeply into the flesh of the finger; two others had compressed the nail sufficiently to make some bruises underneath, and two teeth of the upper maxillary had been deeply fastened in the tissues. The wound bled profusely; it was washed freely with water for about ten minutes; and as the pain was violent, we applied a compress soaked in ether to the finger to try to moderate it. It irradiated from the middle and spread on the whole median nerve pathway as far as and including the arm pit. At the same time a purple-colored swelling appeared extending from the end of the index finger to the wrist, following the inside edge of the dorsal

side of the hand. But in this local action, the periphery of the wound was surrounded by a pale zone, such as is observed around the sting of vespids.

"General symptoms followed nearly five minutes after the bite; they began with a profuse generalized perspiration, paleness, mottling of the face, and faintness; but neither nausea nor vomiting developed.

"The phenomena of dizziness were lessened a little at the end of about an hour, so that I could return home where the faintness and profuse sweating reappeared. The feeling of weakness obliged me to lie down, since I would soon have to get up again to receive Dr. Desgrez, who, having been informed of the accident, was coming to help me. At this moment, the local pain was a little lessened, the general symptoms seemed to have passed when without warning, while speaking, I suddenly lost consciousness. During the one minute approximately that the fainting spell lasted, there were some slight convulsive movements. After I revived, the profuse perspiration reappeared, and also the sensation of weakness, which disappeared with rest in bed. The critical phase of the venom's action lasted about three hours.

"With regard to the local pain, it continued quite sharply in spite of the moist bandage on the hand; but the purple swelling that followed did not extend beyond the wrist.

"In the following week, the local pain persisted with aggravations due without doubt to the irritating action of the venom remaining deep in the wound, because the latter had made good progress and showed no secondary infection; fainting spells still occurred; and the general phenomena: dizziness, asthenia, attacks of numbness, profuse sweating, feelings of weakness at the least exertion, persisted for about five months after the bite.

"I have reported this observation because it is at the present time almost the only one in which the symptoms produced by large doses have been followed. It gives therefore a definite idea of the acute poisoning by the venom of *Heloderma*, which, in these conditions, carried out its most serious action against the heart.

"The mortal dose for man seems to me to be about five milligrams of dried venom; this approximate measure is deduced (1) from the fact that only one bite can lead to death; (2)

from the quantity of venom that one animal can produce at a given moment. The various previous deductions made on six individuals in good health have provided us with the average of five milligrams per subject."

CASE No. 17

A death following the bite of a helodermatid in 1915 is reported by Storer (1931), who obtained rather detailed information, though it is uncertain whether the victim was bitten by *Heloderma suspectum* or *H. horridum*. Storer entertains some doubt concerning the ultimate cause of death, which could have been the result of the intravenous injection of adrenalin. It is uncertain whether the victim was a drug addict, but apparently he had not received any great quantity of alcoholic liquor. However, its use is implied, and because alcohol is almost invariably mentioned in other case histories where death ensued, it cannot be overlooked as a contributing factor. Storer relates the facts as well as his inferences:

"It is of interest, therefore, and also of importance to report a case of poisoning from the bite of a gila monster in which reasonably full data are available and in which the victim died a short time after being bitten. The case chanced to be taken before the California Industrial Accident Commission and full evidence was obtained from all available witnesses. A transcript of the clinical history is also at hand. The record is therefore fairly complete, perhaps more so than in any previous case. The autopsy surgeon's report gives no details which are of value. There are some discrepancies between the medical record and the testimony presented before the Accident Commission but there is substantial agreement on most points.

"L. M. (or L. B.) was a man employed at an amusement place on Main Street, in Los Angeles. Some time in the summer of 1915 the management had purchased a gila monster (*Heloderma* sp.) which was kept as one of the features of the show. Employees had been warned to leave the animal alone, not because of any possible danger to themselves, but because by injury to the animal its value as an exhibit might thereby be reduced. This order had not been enforced, and L. M. had been in the habit of taking the animal to the front of the place and displaying it in order to attract

patronage to the show.

"Having stated earlier to the proprietor and to other employees that he had been bitten by other gila monsters used elsewhere in similar capacity in the past, he entertained no particular fear of the animal. On August 16, 1915, he was holding the reptile in his right hand and at intervals tapping it on the nose with his left hand to induce the animal to open its mouth. Continuing this procedure his attention was distracted by a question from some bystander and on striking down, the index finger of his left hand dropped into the gila monster's mouth. The reptile immediately clamped down on the finger, and, as is the habit of the species, held on with bulldog-like tenacity. Efforts to pry its jaws apart did not avail and so two other employees each seized a jaw and forced them apart so that the finger could be extricated. The man was not alarmed by the event but one of his associates recommended that the wound be treated and an effort was made to obtain a hypodermic syringe. This failing, he was taken to the Los Angeles Receiving Hospital where he came under medical attention.

"As soon as the patient reached the hospital, which was about 15 minutes after having been bitten, the attending physician immediately applied a tourniquet to the afflicted (left) arm, to stop the flow of blood toward the heart. There were two small cuts, on the palmar surface of the distal and middle phalanges, respectively, of the left index finger. These were about half an inch apart and each one-eighth inch in length. Potassium permanganate solution was injected rather freely into the bitten finger around the bites and elsewhere, the physician believing that it was better to run the risk of losing the finger than of injecting an amount too small to be effective. Fifteen minims of digalen (a digitalis preparation) was given as a heart stimulant and then 37 ounces of warm normal saline together with 15 minims of adrenalin were administered by intravenous injection in the right arm. Also, a deep hypodermic of 1/120 grain atropin was given. About this time the patient gave a big convulsion and fell back. Stimulants were applied but to no avail. The patient rallied only to gasp a few times and then die. Death came about 51 to 52 minutes after having been bitten.

"The question being raised as to the patient's having taken a large dose of alcoholic liquor

and that the death might have been due to alcoholic poisoning, the attending physician stated (at the hearing) that the victim had not received any great quantity of liquor. The physician also stated that when the patient entered the hospital he acted like one who had received a dose of poison, with a tremor similar to that observable in typhoid fever and due to a toxic physical condition and not to mental distress. The man was not frightened and did not think that the venom would poison him, this probably because of his previous experiences.

"When the patient first entered the hospital his color was normal. Shortly before the end his lips became blue, then his entire face was blue and when he died he was cyanotic generally. While under treatment the patient remained calm and answered a number of questions put by the physician.

"It should be pointed out that the bites in this case were made on the palmar surface of the finger and that it was the teeth of the lower jaw (with which the venom ducts are associated) which caused the wounds. This circumstance and the fact that the animal kept its jaws closed tightly over the wound, with the masseter muscles contracted, are both of importance in comparing this case with Dr. Shufeldt's experience.

"At the hearing before the Industrial Accident Commission which was brought to recover compensation for benefit of the widow and one child, a number of points of interest were brought out. The deceased indulged in liquor, sometimes to excess, according to testimony of witnesses, but had imbibed no undue amount immediately prior or subsequently to being bitten. He had suffered from a weak heart, being unable to do ordinary manual labor by reason of this infirmity. Both he and two or more of the witnesses had been bitten by gila monsters previously but none of them had ever suffered any great inconvenience by reason of such bites. One of the witnesses for the defense succeeded in introducing oral and photographic evidence purporting to show that the direct bite of the gila monster is not fatal to chickens, guinea pigs or rabbits. In each case the animal bitten lived. No recourse had been taken by the claimant's counsel to scientific literature in an effort to ascertain the effect of *Heloderma* venom in properly controlled experiments. The possibility

of an air embolus having developed at the time of the intravenous injection of the saline solution and having been the cause of death, was brought up by the attending physician when under examination by plaintiff's counsel. The physician answered his own query by affirming that he had taken pains to prevent formation of an embolus.

"The decision by the Commission stated in part 'as to the issue that the bite of the "Gila Monster" is not poisonous, upon which there is a conflict of authority, the fact that death followed so rapidly upon the bite, with other symptoms of poisoning, was found to warrant the decision that the bite was the proximate cause of the fatal result.'

"I submitted the above account to Dr. Herbert C. Moffitt of San Francisco and asked his opinion as to the probable effect of the treatment. Doctor Moffitt stated that the intravenous injection of adrenalin has, in a few cases, been followed by fatal results; also that the rapidity of injection of salt solution and the amount injected is of importance, since in a weakened heart overdistension of the right side may be followed by grave symptoms. Mr. Virgil W. Owen followed up the case independently, immediately after the death, and was told that the victim was a drug addict.

"The alleged physical condition and previous history of the victim, the nature of the medical treatment administered, and the fact that the gila monster had been in captivity for some time (which in the belief of some persons results in lowered toxicity of the venom) are factors which must be considered in deciding whether this death was due directly to *Heloderma* poisoning or whether the poisoning was merely accessory to the final outcome. Despite the detailed record, I feel that the case must be considered as inconclusive. I am led to record the details that physiologists and physicians may form their own conclusions."

CASE No. 18

Through the kindness of Dr. Laurence M. Klauber, we have a clipping from the Arizona Republic of Phoenix, Arizona, for April 29, 1930, which reports the result of a bite inflicted by a Gila monster on a resident of the town of Casa Grande the previous day. The account states, "Tom Reap, 62 years old, proprietor of

the Moore pool hall, died at 12:20 o'clock this noon in the Casa Grande hospital, two hours after he had been bitten by a gila monster. The attending physician said last night that he would give 'poisoning from a gila monster bite' as the cause of death in submitting the death certificate.

"Mr. Reap was playing with the animal in the pool hall when he was bitten. The animal had been brought into the hall by one of the patrons and several were standing around looking it over and discussing it when Mr. Reap appeared. He began tapping it on the nose, witnesses said, and upon being cautioned replied:

'Oh, it wouldn't hurt you even if it did bite.'

"The reptile snapped at Mr. Reap, scratching one of his fingers, those present declared. But Mr. Reap, they said, continued to tap the animal on the nose. They said that suddenly it snapped again and this time sunk its teeth deeply into Mr. Reap's thumb. It required five minutes to get the reptile loose, the men finally succeeding with the aid of a pair of pliers.

"In the meantime Reap became unconscious.

"He was taken to the Casa Grande hospital where he was given immediate care. He regained consciousness but his condition was weak and all further efforts to save him proved futile. He again lapsed into unconsciousness and died at 12:20 o'clock."

Three months later an informant supplying details omitted from the account for obvious reasons wrote "I investigated this, and it is all too true. Completely paralyzed within about 2 minutes. The Dr. said he never saw anyone throw up such stuff or pass from bowels [*sic*]. Said he could hardly stay with him. The man was drinking, and may have been quite drunk, so witnesses said." The case is apparently the same one referred to by Arrington (1930) as "handled by a competent physician and yet the patient died within three hours after the attack." Mulch's (1952) note that "the only fatality from this animal's bite on record occurred in 1930" doubtless refers to the same case.

CASE No. 19

Mr. C. L. E., a dealer in live reptiles who maintained an establishment in Phoenix, Arizona, was bitten on July 24, 1940. He wrote an account of the incident to Dr. Laurence M. Klauber, who generously placed the letter at

our disposal. The dealer writes, "I got my second Gila bite last evening, as I was unloading three out of a box. It was a foolish move, but a hold I have taken, of hundreds of them. I was reaching for him, as he was lying in the box, with his head up, in a corner. Reached for the back of the neck, with the palm of my hand just above his nose and just the instant I touched his neck—SNAP, BANG, he threw his head up, and back, and caught the ball of the thumb, and involuntarily, I jerked up, and tho he had a good mouth full I threw him about ten feet up.

"The pain was there instantly, and quite severe, as he was particularly vicious, and shut down with all his might. He was very mad, as had been hauled about 15 miles, with two others in a box. Being a tough spot, laceration was slight, but holes were deep. Blood came almost instantly, and soon flowed considerable. I stepped into the house, and washed it quickly, and soaked it in mercurochrome, and bandaged it nicely and suffered considerable pain, about six hours. Okay this morning, with very little swelling."

CASE No. 20

Without providing other details, Arrington (1930) mentions "a fourteen year old boy was bitten with no more serious result than a swollen arm."

CASE No. 21

"Fortunately the writer has been bitten but once by the poisonous lizard, and that by a youngster hardly eight months old and far from maturity. In fact, the animal was considered too small to be of any danger, and on the occasion of the bite it was placed in the left shirt pocket while the writer was momentarily examining another specimen. Probably attracted by the breathing motion of the chest, the baby reptile bit into the flesh, immediately below the heart, and held on until forcefully removed. This took approximately a minute, so powerful were the youngster's jaws. Three teeth went through the cloth of the shirt and undershirt and entered the flesh. Considering the bite of little consequence, the writer merely cleansed the wound with an antiseptic and continued the work at hand. However a few minutes later small pains were felt in the region of the bite,

and a slight swelling began. An increased heart action was also noticed at this time.

"The bite occurred at about nine thirty in the morning, and the pain and swelling increased until noon, though at no time were either alarming. An area covering the wound, the size of a half dollar, turned a bluish hue similar to the discoloration found around a snake bite. At three o'clock the pain seemed to start diminishing, but until ten hours later a noticeable agitation remained. Difficulty was experienced in using the left arm, and this condition persisted to a slight degree for two days, after which all effects had left except for a slightly darkened coloration around the bite. This remained for some time." (Arrington, 1930.)

CASE No. 22

Taylor (1938a) tells how he was bitten by *Heloderma suspectum* shortly after capturing two specimens near Guaymas on the coast of Sonora, México.

"This last specimen was captured and placed in a sugar sack. On picking up my 'snake stick' which had fallen near the sack, the *Heloderma* made a quick lunge, and seized the third finger of my right hand, sinking the teeth to the bone. With a quick jerk, I tore my finger from the animal's mouth, thus widely opening the wounds. After sucking the wounds, the fingers were wrapped up and collecting continued. There was no ill effect, other than that which any wound of like extent would cause. No effects that could be attributed to venom could be observed."

CASE No. 23

A clipping from a New York City newspaper that appeared not long prior to 1940 bears the title "Myron the reptile expert is twice bitten but not shy." It tells how an "18-year-old Brooklyn herpetologist" bitten the day before by a rattlesnake is almost completely recovered, but months longer will be required for him to "recover from the wound to his professional pride." For the rattlesnake bit him "just as he was about to recover from the ribbing he got two years ago when one of his Gila monsters nipped him." The bite from the Gila monster was evidently not serious, but owing to the rarity of such occurrences in Brooklyn, it may

have been mentioned in the daily press—as the “victim” probably hoped it would be.

CASE No. 24

Few details are supplied in the following account, which appeared in a Phoenix, Arizona, newspaper, *The Arizona Republic*, on July 9, 1943: “When a youth with a Gila monster in his hands walked into Sara and Jim’s Cafe at 1605 N. 15th Ave., no one batted an eye said Police Patrolman Bob Scott.

“They just gave him a gallon pickle jar he requested to put the 18-inch-long desert reptile in.

“But the monster wasn’t happy with the idea.

“He bit Norman Matlock, 16, Tolleson, on the right middle finger as Matlock was forcing him into the jar. Matlock’s friend, Frank Ross of Avondale, took the lad to St. Joseph’s Hospital.

“Scott said Matlock told him he caught the reptile in the 1600 block N. 16th Ave. [Phoenix].”

CASE No. 25

A bite mentioned by Woodson (1943a) apparently refers to an individual unmentioned elsewhere, although it is not unlike other cases reported. “One tells of a healthy man, about 20 years of age, who captured a Gila monster and was seized by the thumb as he attempted to thrust the creature into a sack. The lizard released its grip only after the man’s companion pried its jaws apart with a screw driver. A doctor treated the bite about 30 minutes later, and ‘recovery was prompt.’”

CASE No. 26

Woodson (1950) gives the following information concerning a bite incurred under rather unusual circumstances:

“If you want to know how it feels to be poisoned by a Gila Monster, consider the case of the 20-year-old hitchhiker, who as he traveled from Phoenix north on Highway 89 discovered one near Wickenburg. He did not know its nature. So he picked it up, placed it in the bosom of his shirt and carried it there for the rest of the day.

“The next morning about 8:30 he had reached Highway 66 midway between Ashfork and Williams, when, for some reason the

monster became irritated and bit him in the abdomen. It held on with such firmness that when he pulled it loose, his flesh came away with its jaws. He was critically ill when a passing motorist picked him up a few minutes later and brought him to the office of a doctor in Williams. The doctor administered to him for more than an hour; then had him removed to a room in a hotel. ‘He was seized by a paroxysm of vomiting immediately after being bitten,’ the report states, ‘and these attacks continued at close intervals for hours afterward.’”

The same case is mentioned earlier by Woodson (1943a) where a brief account is provided: “. . . a young man, who ignorant of the nature of the Gila monster captured one and tucked it inside his shirt in order to carry it easily. The wound appeared infected and inflamed, and the patient suffered a moderate degree of pain and shock.”

CASE No. 27

A bite that occurred in Tucson, Arizona, in July, 1948, was described by the victim (in a letter dated December 6, 1948) as follows:

“I was bitten by one of my Gila Monsters. Although it was a mere baby, some ten inches long, it put me in the Veterans Hospital for five days and my hand and forearm was far from well when I got out. I was bitten on the knuckle of my left index finger and although only the anterior lower and upper teeth made contact, the lower anterior gave me enough venom to make my hand and forearm swell to an enormous size by the time I got to the hospital one and one-half hours after the accident. I did not call the doctor for half an hour after the accident because I did not think it would be serious since I managed to remove the monster about fifteen seconds after it made contact. I can assure you I was a very sick man that day. I vomited from 11:30 A.M. to 8:30 P.M. and my WBC went up to 16,750. by the time of my arrival in the hospital.”

An abstract (Tinkham, 1954) of an unpublished account dealing with the same incident provides additional information:

“The toxicity of Gila monster (*Heloderma*) venom is the subject of controversy. The author described his own experience in having been bitten by a baby specimen (8½ inches) and believed less than a year old. It was in poor

condition. The site of the bite was the first knuckle of the left hand; the teeth involved were the extreme upper and lower anterior, which heretofore have been considered non-poisonous. The victim was in excellent health, with no known allergies. Contact with the knuckle occurred for only 12 to 15 seconds, and mouth suction was instantly applied; later, ice was applied, and three tourniquets every ten minutes during cryotherapy. Nausea and vomiting began within an hour, continued for four hours, then gradually subsided. Within two hours of the bite the hand and forearm were extremely swollen and painful to the touch; sides of tongue were swollen, cyanotic; breathing labored. Phlebitis-like streaks appeared on upper arm. No treatment was administered except injections of penicillin, and 2 liters of physiological saline. Swelling gradually receded over several days; the patient was very weak.

"*Heloderma* venom, therefore, is extremely poisonous, since apparently only a fraction of a drop was injected. The venom appears to be a myelotoxin with little evidence of neurotoxins present. The lymphatics seemed not much involved."

CASE No. 28

Duellman (1950), who was present when a Gila monster managed to engage its teeth in a human victim, describes the incident:

"A Case of *Heloderma* Poisoning.—On June 15, 1948, I had the opportunity to witness a bite by the Gila monster, *Heloderma suspectum*. The incident took place in the Dayton Public Library Museum, where Maurice Fitzmaurice was handling a 15-inch specimen that had recently been received from Tucson, Arizona. Fitzmaurice was reaching past the lizard to the water dish in the cage, when without warning the lizard quickly turned and seized part of the middle and distal phalanges of his right forefinger. Holding on tightly it chewed slowly, working its teeth deeper into the flesh.

"I tried to pry open the lizard's mouth with a mechanical pencil, but to no avail. Finally a full five minutes after the bite occurred, Fitzmaurice slammed the lizard to the floor and pried at its mouth with his left thumb. The lizard momentarily opened its mouth, and the victim withdrew his finger. He was immediately

bitten on the left thumb, but was almost instantly released.

"In the meantime Fitzmaurice's finger had begun to pain him. He held his hand under running water for a few minutes in an attempt to wash away the saliva and possible venom. There was slight bleeding from the four punctures in his right forefinger and the two in his left thumb. By now the forefinger was beginning to swell, and he experienced considerable pain in his whole right hand.

"We walked to a doctor's office three city blocks away but were unable to obtain help. By now the forefinger and much of his right hand as well as his left thumb had become decidedly swollen. The punctures were still bleeding, and throbbing pains had commenced in his right hand. There were distinct signs of nervousness and shortness of breath. A police car was called and at 5:00 P.M., just thirty minutes after the bite occurred, we reached the hospital. Occasional pains were felt in the right arm, and the pain in the right hand and forefinger had become intense.

"At 5:15 P.M. the following treatment was given at the Miami Valley Hospital: the wounds were cleaned, and 1/6 grain of Morphine Sulphate was injected hypodermically into the *thenar eminence* of the right hand. When the morphine had taken effect, the punctures were lanced. One of the teeth had punctured the nail of the forefinger. This was split so that the wound could bleed freely. All of the wounds were treated with an antiseptic. Six times during the next twelve hours 50,000 units of Penicillin were injected intramuscularly.

"Fitzmaurice was released from the hospital on the following morning. At that time the dorsum of his hand was only slightly swollen, and he did not complain of any pain."

CASE No. 29

Shannon (1953a, 1953b) has supplied two accounts of a bite inflicted on himself. In the first account he states, "The venom is largely neurotoxic in action, and judging from the gravity of results seen in bitten laboratory animals it would be well to treat a Gila monster-bite with the same thoroughness as a snake bite. The author was bitten through a sack in the fall of 1952. The wound was a quick slash through the pad of a finger, and the animal did not get

a chance to hold on and chew. For a half hour there was a local pain which was not excruciating. Little swelling resulted. Systemic effects were slight and consisted of nausea which was probably due to pain, tachycardia (not entirely due to pain, as it persisted at a rate of 120 after two hours), and a slight bilateral tinnitus occurring after an hour and lasting most of the day. The wound bled freely and still bled upon exertion of the finger three days later. Clotting time of the escaped blood was not prolonged."

As described later the same year, "The author was bitten by the same Gila monster [the one mentioned in Case No. 30 below] when he inadvertently grasped the sack containing the lizard. The bite was through two layers of cloth and was inflicted as a momentary, slashing wound a quarter-inch deep on the terminal phalanx of the third right finger. The bite was extremely painful for two hours, and a slight swelling was noted which was restricted to the finger. Nausea was experienced but was probably due largely to pain and heat of the day. A slight tinnitus was present two hours after the bite and lasted the rest of the day. No other systemic symptomatology was noted. The finger was painful to pressure for a week, and for three days it would bleed if at all exerted. No prolongation of clotting time was detected in the escaped blood."

CASE NO. 30

A fair percentage of the bites inflicted on human beings by Gila monsters have resulted from the improper treatment or careless handling of captive helodermatids. The case described by Shannon (1953a) involves a victim who was under the influence of alcohol. It is a matter of conjecture whether the alcohol played any role in the moderately severe symptoms observed. Shannon's report follows:

"An 18-inch specimen of *Heloderma suspectum* was acquired in September of 1952 from Dr. Charles Lowe of the University of Arizona. The lizard was captured by Lowe at Tucson and had been used by him for certain physiologic studies. It had not been harmed in any way. The lizard was carried to three different army posts during the course of the winter and spent considerable time in a sack, cages being built as frequently as possible. Feed-

ing was infrequent, but the animal's metabolic activities were not high as it was usually in a torpor caused by the chill of night. For the past month the lizard has been in a cage at Camp Desert Rock, Nevada, and has had frequent feedings of raw eggs. At the time it inflicted the following bite it was in good condition although demonstrating the usual sluggish nature of captured specimens.

"On the night of March 19, 1953, an officer removed the Gila monster while the author was away and carried it to the officers' bar, where he proceeded to put on a wild animal show. The officer's cupidity, increased by recent imbibition of two beers, six martinis, and five scotch-and-sodas, caused him to indulge in a game of Russian roulette, which was to have consisted of poking his right index finger into and out of the Gila monster's widely opened jaws. The first attempt was unsuccessful, and the lizard bit him firmly on the finger at the junction of the nail. After suffering three or four more good bites, each more distal than the preceding, the officer was able to pry loose his lacerated and freely bleeding finger. It was estimated that the lizard had indulged in a successful chewing time of some six or seven seconds. After freeing his finger and being startled into momentary sobriety, the officer vigorously milked his arm, hand, and finger in an attempt to express as much venom as possible from the bleeding terminus. A rather tight tourniquet was applied within minutes to the finger, and for a feeling of extra security, two or three more were applied extending up the forearm. The tourniquets were removed at intervals during the 45 minutes following the bite which occurred at 10:30 P.M. and were off at the time of the author's arrival at 11:00 P.M. One of the medical aid men gave the officer 0.3 cc. of adrenalin intramuscularly at 10:50, fearing that he would go into shock. On arrival the patient was found sitting up on an examining table drinking coffee and suffering considerable pain. The pain had not been noticed until a few minutes preceding but was probably only masked as large amounts of alcohol are amazingly effective in producing effective analgesia. The patient's blood pressure was 190 systolic and 90 diastolic and his pulse rate 92. The patient was apprehensive and by 11:05 P.M. his pain was so severe that a quarter grain of

morphine tartrate was given intramuscularly. As the patient was a large, young, strong, and obviously healthy male (75 inches, 220 lbs., 29 years old), incision and further application of the tourniquet were not employed. Difficulty was experienced in obtaining a good subjective history as the patient's sensorium was masked by alcohol. It was noted that his hand and the first three or four inches of his arm were moderately swollen and hyperemic, and that considerable swelling existed in the index finger. Both swelling and pain were greater than could have been caused by the tourniquet.

"By 11:45 P.M. the effects of the adrenalin had diminished to the point that the patient's blood pressure was down to 146/76 and the pulse rate was 72 beats per minute. One gram of streptomycin was given intramuscularly at this time as well as a booster dose of one-half cc. of tetanus toxoid. The pain was pulsating in nature, shooting up the arm to the height of the deltoid insertion, while a steady burning pain was superimposed in the injured finger. At midnight a half-grain of intramuscular codeine sulfate was administered. At this time a blood count was performed and a mild leucocytosis of 11,700 was noted. The differential count of 54 neutrophils, 44 lymphocytes, and two eosinophils was within normal limits, although slightly high in lymphocytes. Correct evaluation of the leucocytosis is difficult as both alcohol and reptile venom may produce it.

"The pain increased steadily until 12:50 A.M. in spite of the morphine and codeine. As it was now felt that central nervous symptomatology due to the venom would be minimal, another quarter grain of morphine was given. At 1:00 A.M. the lacerated finger was dressed and the patient removed by stretcher to his quarters. He was exhausted by walking a few feet to his bed, his respirations increasing from 22 per minute to 45. His staggering gait was undoubtedly due to morphine, codeine, and alcohol, but it is not likely that these substances were responsible for the hyperpnea. The blood pressure checked 126/76 and the pulse had increased to 90. Within five minutes both pulse and respiration diminished to normal and the patient dropped off into an uneasy slumber. Blood pressure, pulse, and respiratory checks were made at three different times during the night and were found to be normal. The pa-

tient does not recall these visits, and as he was not unconscious no serious attempt was made to awaken him.

"The patient slept throughout most of the next day, and when awake he was weak and dizzy and had a dull roaring in his ears which was not marked enough to be termed a tinnitus. The author knows the patient personally and feels that his symptomatology was too marked to be adequately explained by a hang-over from the alcohol and opiates. By the second day the patient was still slightly weak and tired easily, but he resumed his normal activities without undue fatigue. At no time since the second day has the finger hurt when at rest.

"The finger was slow in healing and on the day following the bite was still considerably swollen with a slight purulence under one tooth mark. This responded to continued use of streptomycin and by the third day the hand was improved to the extent that the patient tried using a screwdriver. He had exerted only a slight effort when the lacerations broke open, allowing escape of a small quantity of sero-sanguinous fluid. At this writing, a week after the bite was inflicted, there is a local hypesthesia and pain to pressure."

CASE No. 31

Mr. William H. Woodin, 3rd, Director of the Arizona-Sonora Desert Museum near Tucson, Arizona, has generously supplied us with an account of a bite inflicted on John Pearce, a local high school student. As quoted verbatim from the victim's letter to Mr. Woodin, the account states:

"April 3, 1953 Time approximately 10 A.M.

"*Heloderma suspectum* seen on road the approximate midpoint between Tucson and Three Points on Sells-Tucson Highway. My small dog gets to it first. He is bitten somewhere on the face, no ill effects except for vomiting that night.

"I caught the Gila Monster and put it in a sack. It bit me on the end of the thumb through the sack. It was a sharp pain, much like a Chuckawalla bite. I ripped my thumb loose, then I tied a cloth around my wrist. The bite bled freely for approx. 3 minutes, washing it often. I bandaged it up. The thumb swelled

constantly. Used a constriction band for 15 minutes. In about one half hour or an hour the thumb was swelled so I thought it would burst. I touched my wrist and felt it tender. In a few minutes my whole arm was sore. The nodes became swelled and very sore. The thumb turned blue. I couldn't bend it. By 2:00 P.M. the swelled, sore thumb was all that was left. I could bend it partly. 5:00 P.M. Thumb still sore, could bend almost completely. Next morning thumb only tender. That evening it was only sore around bites. Next morning, 2 days later, healing fine."

CASE NO. 32

In an article explaining why the state of Arizona has seen fit to protect the Gila monster, Mulch (1952) mentions a bite inflicted on a member of the staff of the Poisonous Animals Research Laboratory, Arizona State College, at Tempe. "A popular misconception is that in biting, a Gila monster must grate its jaws for several minutes before poison enters the wound. This is incorrect, according to Dr. Stahnke who speaks from practical experience. He was bitten a year and a half ago by a monster that held on for less than a tenth of a second. The wound was extremely painful but the poisonous effects were combatted effectively with the application of ice—similar to scorpion sting treatment."

CASE NO. 33

For the account that follows, we are indebted to Mr. William H. Woodin, 3rd, who was bitten on September 29, 1953, at the Arizona-Sonora Desert Museum near Tucson, Arizona.

"I had put the creature in a sack and while in the process of tying it, brushed the sack with the side of my left hand. He then nipped me for a fraction of a second, getting me with a few of his anteriormost teeth on the side of the hand one inch below the little finger. There was an immediate burning sensation and a continuous sharp burning pain which began to lessen slightly in half an hour, and was definitely diminishing before two hours' time (after one hour and 45 min. I have in my notes: 'only a little pain if hand held still'). Swelling began about a minute after the bite with a tightening

sensation, and after another minute I noticed throbbing. The bite bled freely for several minutes, and my only treatment was some suction (without incision) and immersion in ice water for about 10 minutes, which made it feel somewhat better at least. The swelling increased until the side of my hand was rather swollen; this never involved more than the side of the hand and was not perceptibly increasing one hour and 45 min. after the bite. One half hour after the bite I have in my notes: 'Area has become tender to touch,' and at 2:00 P.M. (bite was at 12:14 P.M.): 'Area very tender to touch 1½ inches around bite (only ½ inch on back of hand). Hurts severely to clench fist; also painful to straighten hand.' At 3 P.M.: 'Pain nearly stopped unless hand moved. Swelling not increasing. Tenderness not increasing.' 4:00 P.M.: 'Pain stopped unless hand moved.' 6 and 9 P.M.: 'No change.'

"Next morning (Sept. 30) 8 A.M.: 'Little change except swelling mostly receded. Side of hand rather stiff and sore. Tenderness slightly lessened.' 10 A.M.: 'Tenderness lessened.' 8 P.M.: 'Little change. Area painful if hand moved. Often faint burning even if (hand) still.'

"Oct. 1: 'Pain sensation lessened. Very tender to touch on immediate area, but by afternoon can move hand and clench fist without pain. Area surrounding bite not at all tender.'

"Oct. 2: 'Lessened pain sensation. Area of bite not very painful to touch.' The pain sensation decreased over the next few days until it was completely gone on Oct. 6. There was never any systemic reaction. There was, however, some discoloration at several of the tooth marks."

The bite was reported in the Arizona Daily Star of Tucson on September 29, where it says only that "Bill Woodin . . . was putting a gila monster into a bag. As he drew the bag closed the gila bit him on the left hand."

CASE NO. 34

An unidentified writer (Anonymous, 1954) reports a bite from a Gila monster that was incurred by a member of the staff of the Steinhart Aquarium in San Francisco. According to the account Armeka T. Jackson "was nursing a hand that bore toothmarks of a Gila monster,"

described as being "a chunky lizard about 20 inches long" that "had always been considered extremely docile."

While Jackson was cleaning its cage, the lizard was transferred to a round container 2 feet high and 1 foot in diameter. When Jackson "reached in to take the normally torpid reptile out of the box it [the Gila monster] flew into a rage. It bit through Jackson's protective leather glove and into his hand. Fortunately, the lizard didn't get a bulldog-grip which would have enabled it to inject its poison."

The author continues, "When events were reconstructed in the curator's office, Jackson

remembered that the week before a stump-tailed skink [supposedly *Tiliqua rugosus*] had expressed extreme displeasure after spending a few minutes in the same box. And the same had been true of a Mexican beaded lizard [*Heloderma horridum*]. Like detectives the gentlemen set to work. Upon close examination it was discovered that a bit of delousing powder had somehow found its way into the box."

While the "powder" is not identified, some insecticides currently in use contain chemicals that stimulate nerve action. This may account for the sudden change in the behavior of the reptile.

ANALYSIS OF CASE HISTORIES

Of 34 bites reported to have been inflicted on human beings, eight are said to have resulted in the death of the victim. It should not be inferred from these figures that the mortality rate approximates 25 per cent. Aside from the dubious nature of some of the reports, it is probable that numerous minor bites not followed by serious consequences have never been reported or even mentioned in print. Cases where death resulted, or where symptoms were sufficiently grave to warrant hospitalization, would inevitably receive more attention in the press or in scientific journals.

The gravity of a bite depends on several factors, discussed below. The present discussion deals with the cases listed. Because some of the reports are incomplete, while others are of doubtful authenticity, it is questionable whether it is worth while to tabulate the information in terms of percentages. However, we can summarize much of the information.

CIRCUMSTANCES UNDER WHICH BITES OCCUR

Bites have been inflicted on persons:

1. While examining specimens kept alive in laboratories, zoological gardens, museums, or kept for sale, for show purposes, or simply as pets.

2. While removing or replacing Gila monsters in such containers as cages, boxes, or jars.

3. While tying, handling, or merely coming within proximity of sacks containing Gila monsters. In three instances Gila monsters succeeded in engaging their jaws under such conditions. Even though cloth intervened between the

teeth and the flesh, the symptoms following some of the bites indicate that small amounts of venom had been introduced.

4. While restraining a Gila monster trying to escape from bucket over which a towel had been tied.

5. While teasing captive specimens. Some of the more serious cases resulted when the victims, in an inebriated condition, incautiously maltreated Gila monsters.

6. While getting off a horse, to the saddle of which a supposedly dead Gila monster had been tied.

7. While carrying a juvenile Gila monster in a shirt pocket.

8. While carrying a Gila monster in the bosom of a shirt, not realizing that the lizard was venomous.

9. While attempting to brush off a Gila monster that crawled over the victim as he lay asleep in a cave.

10. While exhibiting a helodermatid to entice customers into a place of amusement.

11. While "in the field" or "while prospecting," allegedly bitten, respectively, "on the foot" and "just above the shoe." Both cases are unverified.

LOCATION OF BITE

The majority of the bites by helodermatids have been on the fingers. While there is conflicting evidence in some cases, fewer have been on the thumb. Rarely both a thumb and a finger were involved. Two bites were received on the hand proximal to the base of the fingers, two on the chest or abdomen, and one on the wrist. Questionable accounts would also indicate that

victims have been bitten on the foot or just above the shoe.

VICTIMS AND THEIR LOCATION

Few accounts provide information concerning the age of the victims, but it is evident that they ranged from a boy 14 years old to a man of 62. The majority appear to have been young or middle-aged men. Only one woman, Marie Phisalix, is included among the victims in the cases assembled.

The Gila monster is more likely to be encountered in Arizona than in other regions, with the possible exception of the Mexican state of Sonora. In Nevada, Utah, and New Mexico, where it is both rare and restricted to limited portions of the state, no bites have been reported. As might be anticipated, more bites have occurred in Arizona than elsewhere. Gila monsters still occur within the city limits of such population centers as Tucson. Most of those supplied to zoological gardens in other parts of the world have come from Arizona, where dealers as well as collectors have been bitten. Gila monsters were commonly exhibited in roadside "zoos" in Arizona until 1952, when the lizards became protected by state law. Consequently more human beings were handling Gila monsters in Arizona than in other portions of the globe.

However, in view of the interest in Gila monsters and *escorpiones*, these lizards have been shipped to many parts of the world either for exhibit or study. Bites have been inflicted on human victims in Austria (presumably) and France, and there are reports from the District of Columbia, Arizona, California, New York, Nevada, and Ohio. One bite occurred in the Mexican state of Sonora, while a victim of the bite of *H. horridum* occurred at an unspecified locality in "Mexico."

SYMPTOMS FOLLOWING BITES

No information of value is available for bites inflicted by *Heloderma horridum*. Bites from Gila monsters have resulted in symptoms that vary in their severity from a slight pain comparable to that from a scratch, a cut, or a pin prick to those of considerable gravity. Under exceptional circumstances death may ensue.

In those instances where minor symptoms have occurred, the reptile has usually been able

to engage only a few teeth at the front of the jaws, sometimes with cloth intervening when the lizard was in a sack. Removal was invariably prompt, and in some cases it is probable that no venom reached the blood stream. The pain that resulted was sometimes not severe and can be ascribed to the trauma (the cuts or punctures), or to the bruising of the flesh from the pressure exerted by the muscles of the lizard's jaws.

Cases of moderate severity (such as No. 3 or No. 27) can result from seemingly minor bites involving only the teeth at the front of a Gila monster's jaws, even those of a juvenile. In such cases it may be assumed that a small amount of venom was introduced. Severe pains, accompanied by a rapid swelling, faintness, nausea, and perspiration may result.

In more severe cases, particularly those where the Gila monster seized a finger or a thumb and could not readily be removed, similar but usually more severe symptoms have ensued, with acute sensitivity at the site of the swelling, with loss of consciousness in some instances, and with repeated vomiting in others. Accelerated heart action and shortness of breath are sometimes present. Pain, vertigo, numbness, and a feeling of weakness may persist for several days after a bite. The swollen tongue and the impairment of glands in the throat (Case No. 6; a swollen tongue is also mentioned in Case No. 27) or subjective noises in the ear (the tinnitus of Case No. 29) may be exceptional symptoms, or they may have been overlooked in other cases.

It is noteworthy that swelling is reported in virtually all cases where more than a few teeth penetrated, or where the accompanying pain was too severe to be attributed only to the wound inflicted. Cooke and Loeb (*in* Loeb *et al.*, 1913) assert that swelling at the site of the bite is not due to "the toxic principle," but may perhaps be attributed to mechanical injury, to the presence of pathogenic organisms, or to the admixture of other secretions from the lizard's mouth. The presence of pathogens may account for the swellings observed in human victims, where mechanical injury alone has been insufficient to produce the symptoms reported. As noted in the previous section, Phisalix (1914, 1922) concluded that the venom of the Gila monster contained at least two active sub-

stances, one of which was destroyed by heat. Therefore, it is possible that the use of heat in sterilizing the venom employed by Cooke and Loeb in their experiments destroyed toxic substances in the venom even though the neurotoxin was virtually unaffected. Swelling, ecchymoses, and hemorrhages were observed in rabbits and rats into which fresh venom, unsterilized, was injected. If proteolytic enzymes are present in the venom of *Heloderma* (as implied but not substantiated by Shannon, 1954a), these elements as well as the pathogens may have been inactivated by heat so that their effects would have been absent in animals into which sterilized venom was injected.

The local effects of a bite, aside from the crushing action of the jaws or the wounds produced by the teeth, may be painful or even serious. But the real danger lies in the systemic effects that can be attributed to one or more neurotoxic elements in the venom.

In regard to the deaths reported from bites by Gila monsters, it is noteworthy that many of the symptoms that preceded death have also been observed in human beings where the outcome was not fatal, or in mammals tested experimentally. Cooke and Loeb (*supra cit.*) point out that disturbances resulting from injections of venom are not identical in all species. Furthermore, similar dosages of venom do not always produce the same symptoms in all individuals of a single species. Variable effects from the venom are to be expected in human beings, where the nature of the bite varies from case to case, and no two victims are identical in size or physiological condition.

The information available for cases Nos. 5, 8, and 9 is too meager to be of value. Few symptoms are mentioned in some of the remaining accounts (Cases Nos. 1, 4, 10, 17, and 18) of bites that preceded the death of the victim, but many of the symptoms that are mentioned have been reported for other animals. The miner of Case No. 1 is described as being paralyzed on one side after being bitten. Cooke and Loeb report that in mice injected subcutaneously with venom, one leg became completely paralyzed when the other was only partly affected. The miner did not die until about three months later. Phisalix (1912a) mentions a hedgehog that survived injections of the venom but later became emaciated, losing one-

fifth of its original weight. Similar effects were observed in a cat exposed to the bite of *Heloderma horridum* by Sumichrast (1880a). The delay in the miner's death, therefore, does not preclude the possibility that it was the result of the venom received at the time he was bitten.

In each of the other cases (Nos. 4, 10, 17, and 18) death occurred so soon after the bite (within 52 minutes to a few hours at most in the case of Colonel Yeager, where accounts disagree), that the effect of the venom can scarcely be ignored as the most likely cause. The case (No. 17) described by Storer (1931) is a possible exception in view of the intravenous injection of adrenalin and other possibilities cited. But even Storer's account mentions the cyanotic condition of the victim at the time of his death, and similar symptoms have been reported (Tinkham, 1954) in non-fatal cases.

Alcoholism may have been a contributing factor in some of the deaths, and none of the victims, with the possible exception of Arthur James (Case No. 10), appears to have been in a state of good health. The victim described in Case No. 18 was 62 years of age, and Colonel Yeager of Case No. 4 is described as being 55 years old and a chronic alcoholic. Information concerning the health or the age of Arthur James is not supplied in the account, but, as he received a more severe bite than any of the others, there is greater likelihood of the venom's having been the direct cause of his decease.

The feeling of weakness, loss of consciousness, and discoloration and swelling at the site of the bite, even the vomiting, micturition, and defecation reported prior to some of the deaths, are all symptoms that Van Denburgh (1898), Van Denburgh and Wight (1900), Cooke and Loeb (*supra cit.*), or Phisalix (1922) observed in experimental animals. It may reasonably be assumed that such symptoms arose largely if not directly from the effects of the venom. Whether there were complications from the introduction of pathogenic organisms in the wounds from the lizard's teeth, or whether the treatment in some cases contributed to the death of the victim, the fact remains that deaths have followed bites by helodermatids in a sufficient number of instances to leave little doubt that under special circumstances a bite can be extremely dangerous.

The quantity of venom necessary to kill a human being may not be so little as the 5 milligrams (dry weight) suggested by Phisalix (1922) as the minimum lethal dose for a man weighing 60 kilograms (*ca.* 132 pounds). But in view of the deaths reported, it is equally uncertain whether it is necessary for a Gila monster to introduce as much as a half a cubic centimeter of venom into the wound in order to kill an adult, as Loeb (1921) hypothesizes.

To ascribe every death reported to the victim's having had a "weak heart," or to his

having been a chronic alcoholic, or a drug addict may help to explain the physician's failure to save the victim's life. But if it be realized that a relatively small quantity of venom can result in the death of a human being, no rationalization is necessary. A man on the gallows may have suffered from a large number of ailments, but the immediate cause of his death is the rope that happens to be around his neck when he can no longer resist the forces of gravity as the support beneath his feet is withdrawn.

FACTORS AFFECTING GRAVITY OF BITES INFLICTED BY HELODERMATIDS

The symptoms resulting from bites of *Heloderma* indicate that their gravity varies from local pain that can be attributed to a simple scratch, puncture, or cut inflicted by the teeth to severe systemic effects or, rarely, even to the death of the victim. In most instances it is impossible to ascertain by an examination of the wound whether any venom has been introduced. The symptoms that follow a bite may, of course, provide clues. Some of the more important factors that help to account for the variable effects of bites include the following:

1. It is of paramount importance whether several teeth, particularly the larger teeth of the lower jaw, are engaged in the flesh of the victim. Because the ducts leading from the glands to the mouth pour out the venom adjacent to the largest and most deeply grooved teeth in the lower jaw, the quantity of venom carried into the wound will tend to be greater if these teeth are embedded in the flesh of the victim. There would be less danger from the teeth in the middle of the upper jaw, the shallower grooves of which are less likely to contain venom; any that reaches the grooves in these teeth must be drawn in by capillary action from the venom that flows out into the pockets of the gum tissue in the lower jaws (see description of the venom apparatus). Finally, the much smaller teeth at the front of both jaws are not only very feebly grooved but are farther removed from the source of venom within the mouth. These smaller anterior teeth probably are sometimes devoid of venom. Under such conditions a bite involving only these teeth might easily fail to introduce any venom into the puncture or punctures produced. Also, some

of the teeth in any part of the jaw may have broken off prior to the bite, particularly if the lizard inflicting it has been maltreated either while being captured or while in captivity.

2. The quantity of venom introduced into a wound will depend on (1) the length of time that chewing continues before the jaws can be disengaged by the victim, (2) whether venom has been extracted or expelled for other reasons immediately prior to the bite, and (3) the condition of the lizard. Gila monsters that have not been well fed, or that have not been kept under ideal conditions in captivity, tend to produce less venom than freshly captured or well-fed animals. Helodermatids past their prime may also produce less venom, or venom of reduced toxicity, although there are no data to confirm this assumption for venomous lizards as there are for snakes.

3. The extent of the irritation of the lizard prior to the bite may be a factor of importance. It seems probable that the venom glands of a lizard that has been disturbed or stimulated may have poured venom into the mouth before the lizard actually engages its teeth. Furthermore, the hissing of an angry helodermatid may serve to distribute the venom to other parts of the mouth, where it may reach the grooves of the teeth in the upper jaw or those at the front of the mouth. A helodermatid that has been aggravated for some time prior to engaging its teeth can probably inflict a more dangerous wound than one not previously disturbed.

4. The size of the helodermatid inflicting a bite is a matter of importance. A large individual would tend to produce more venom and have longer teeth than a juvenile. It has not been

ascertained whether there is any difference between the venoms of the two species, or whether the toxicity varies with the age of the lizard. However, painful bites have been inflicted by juvenile Gila monsters, the bites of which are manifestly dangerous, even though their glands can scarcely contain large amounts of venom.

5. Pathogenic organisms were present in the mouths of Gila monsters examined by Rivas (*in* Loeb *et al.*, 1913), who also found pus-forming bacteria to be present. Some of the pathogens cultured by Rivas proved to be extremely virulent. Deaths or serious symptoms following some bites possibly can be attributed to the organisms rather than to the venom introduced at the time of the bite. Or deaths may have resulted from the combined effects of the venom and the pathogens.

6. The gravity of the bite will depend on whether the victim is protected at the site of the bite by clothing, or bitten through a sack containing the reptile. Any fabric interposed between the teeth and victim would inhibit the penetration of the teeth, with less danger of venom's being carried into the wound. Leather of some thickness might be penetrated by the mandibular teeth of a large lizard, but there would be less danger of venom's being introduced.

7. The size, vigor, and health of the victim would be of importance in determining his resistance. In general the recuperative powers of human beings diminish with age, which may also be listed as a factor to consider. Case histories suggest that more serious symptoms often ensue when the victim is aged or in poor health. Alcoholism may be a contributing factor in some instances, but severe symptoms or deaths following bites can be attributed in part to the lack of caution exercised by inebriated individuals. Such persons are prone to be more severely bitten and can scarcely be expected to be very efficient in removing the jaws of an infuriated lizard.

8. The site of the bite or the portion of the victim's body seized by the lizard is of importance. There would be greater danger of the venom's reaching the blood stream if a person were bitten on a heavily vascularized area, such as the wrist. Most bites occur on the fingers or thumb, where the jaws could

more readily be disengaged than would be the case were the bite inflicted on the wrist. Bites have occurred on the chest, where a helodermatid could not easily engage many of its teeth, but where the venom would be introduced closer to the organs affected by the neurotoxic elements.

9. The victim's susceptibility to a reaction from proteins may introduce complications. Cooke and Loeb (*in* Loeb *et al.*, 1913) failed to induce any anaphylactic reaction with repeated injections of sterilized venom into experimental animals. However, fresh venom may contain elements producing an anaphylactic reaction.

10. The extent of the bleeding from the punctures of the teeth embedded may be enhanced if there has been a sudden withdrawal of the extremity bitten. Venom would tend to remain in a puncture, whereas profuse bleeding from cut-like wounds would result if a digit were forcibly removed in a direction lateral to the teeth. The outward flow of blood from the wound tends to carry with it any venom that had been adhering to the teeth at the time of their penetration.

11. The psychological condition of the victim is important, as apprehension or fear on the part of the victim will accelerate the action of the heart and may affect the rapidity of the absorption of the venom. Extreme fear may also be a factor involved in shock, which may be difficult to combat.

12. Finally, the nature of the first-aid measures, aside from the removal of the lizard's jaws, would affect the outcome of the bite. Suction, whether mechanical or by mouth, tends to remove small quantities of venom, and the application of a tourniquet would conceivably delay its absorption, although such measures may be of doubtful efficacy in delaying the action of neurotoxic elements in the venom. Complications may be introduced by the administration of folk remedies, the use of cutting instruments not previously sterilized, or by such outmoded treatment as the injection of a solution of potassium permanganate.

On the whole the gravity of the bite will depend more on the extent and the duration of the grip obtained by the helodermatid than on other factors, particularly if the lizard inflicting the bite is a large, vigorous animal. Painful

symptoms can result where relatively few teeth at the front of the lizard's mouth are engaged. Grave symptoms are likely to be experienced, however, only when there is a prolonged bite on a person of small size, especially when the

largest teeth in the lower jaw are embedded in a heavily vascularized portion of the body. Sufficient caution is ordinarily exercised by people who handle helodermatids to avoid such bites.

TREATMENT OF BITES INFLICTED BY HELODERMATIDS

Serious bites from helodermatids are so infrequent that there has been insufficient demand for an antivenin to warrant its production. The exploratory experiments reported by Phisalix (1914, 1922) suggest that an antivenin to counteract the effects of the venom of *Heloderma horridum* and *H. suspectum* could be produced. However, the results obtained by Cooke and Loeb (*in* Loeb *et al.*, 1913) indicate that difficulties might be encountered before a satisfactory antivenin could be obtained.

The extensive investigations of the venom of *Heloderma* carried out by Loeb and his collaborators (Loeb *et al.*, 1913) were avowedly "more purely scientific and of comparatively slight practical importance." While these investigators supply information of theoretical importance in dealing with the effects of a bite, they did not devote any attention to the problem of treating a victim. No experimental work has been done to ascertain whether the venom of *Heloderma* can satisfactorily be drawn from a wound by means of suction, nor is it certain that application of a tourniquet is effective in delaying the absorption of any of the toxic principles theoretically contained in the whole venom.

In prescribing suitable treatment for the bites of the Gila monster and the *escorpión*, therefore, we are forced to rely upon such inferences as may be drawn from our knowledge of the venom, the venom apparatus, and the limited information obtained from the reports of physicians who have actually had experience in treating human beings suffering from the effects of the venom.

Diagnosis would appear to be no problem. Ordinarily there is no question concerning the species of animal that produced the wound. Shannon (1954a), however, cites the case of an infant less than two years old who was found unconscious in a cotton patch near Good-year, Arizona. When found, the child was bleeding profusely from a puncture wound on

the left side of the bridge of the nose. It was uncertain whether the child had been bitten by a snake, and one consultant present at the autopsy believed that the bite had been inflicted by a Gila monster. However, as Shannon points out, virtually all the evidence belied this conclusion; it was far more probable that the child died as the result of being bitten by one of the larger rattlesnakes inhabiting the area. Nevertheless, a child could be bitten if he attempted to seize a Gila monster or an *escorpión*, and, if help were not immediately available, it might be difficult to determine whether the bite was that of a helodermatid.

Virtually all the dangerously venomous snakes inject their venom through tubular fangs, with the venom forced into the tissue under a fair degree of pressure. When so introduced, the venom spreads rapidly from the point of injection. Some venom can be removed by incision and suction in the general area, but it is difficult to remove any appreciable amount by making an incision and applying suction at the place each fang penetrates. Fortunately for the occasional victim, the nature of the venom apparatus in helodermatids precludes the possibility of the venom's being injected under pressure. There may be a mild pumping action as the result of the lizard's partially releasing its grip and re-exerting the pressure of its jaws. But on the whole the venom is drawn into the wound along the grooves in the teeth largely as a result of capillary action. There is, therefore, greater likelihood that some of the venom can be drawn out if incisions are made at each place where the teeth have penetrated the skin. The flow of blood would also tend to wash out any venom adhering to the edges of the punctures produced. In view of these circumstances, cutting and suction are likely to be more efficacious in dealing with the bite from a Gila monster or an *escorpión* than would be the case were the victim bitten by a snake.

Stahnke (1953a) questions the value of in-

cision and suction in treating the bites or stings from venomous animals, advocating instead the use of tourniquets and iced water. Stahnke's account is reproduced by Reed (1953), and was republished with minor modifications in a copyrighted article that appeared later the same year (Stahnke, 1953b) in a third journal. Stahnke refers to the treatment he advocates as the "L-C method," having reference to "ligature and cryotherapy," or the use of a tourniquet and iced water.

Assuming that the bite occurs on an extremity, Stahnke (1953a) recommends the application of a tight tourniquet as near the site of a bite as possible, without any incisions being made. According to this author, after the ligature has been applied, a piece of ice should be placed on the site, while a vessel of crushed ice and water is made ready. The bitten member is then immersed in the iced water well beyond the tourniquet. For the bite of a Gila monster immersion for six to seven hours "was found to be necessary," with the ligature removed five minutes after the bitten member is placed in the iced water.

Stahnke also recommends that, if available, ethyl chloride be sprayed around the site of the bite, encompassing an area approximately 3 inches in diameter. Care should be taken not to freeze the tissue, he points out, adding that this can be accomplished by "spraying only to the point of frost formation." When the frost disappears the spraying should be repeated. After the area has become thoroughly chilled, it can be maintained in that condition with an ice pack.

While there are implications that his conclusions were reached as a result of experimental test, Stahnke does not explicitly mention any experiments or clinical testing of his treatment. He adds some theoretical considerations, noting that by reducing the temperature of the tissue to "about 4-7° C." the following advantages are to be gained: (1) the chemical activity of the venom is greatly reduced; (2) the venom "is so held that it will enter the body very slowly"; (3) harmful bacteria introduced with the venom "cannot multiply"; and finally (4) "we also have the anesthetic action of the cold." Stahnke concludes his account with the assertion that "death can be prevented with the L-C treatment alone if sufficient time is given for its use."

Shannon (1953b), however, doubts that ethyl chloride would be effective unless the surface layers of the skin were frozen solid, adding that "there is enough anoxia and histolysis in the region of a bite without aggravating it by excessive cold, heat or surgery. A tourniquet will achieve the same effect more safely and easily."

Furthermore Shannon considers it to be extremely dangerous to lower the tissue to temperatures even approximating the 4° C. to 7° C. recommended by Stahnke. Shannon observes that tissue metabolism is seriously reduced when the temperature of the skin drops to 25° C., and at 15° C. the metabolism of the tissue is so markedly decreased that there is a reduction of dissociation of oxyhemoglobin resulting in a deceptively pink, well-oxygenated appearance of the skin. Shannon continues, "Available evidence indicates that tissue survival at this temperature is slight. Immersion extremity is characterized by a cold, anaesthetic member which changes abruptly in the hyperemic period to a hot extremity with intense burning and shooting pains. The affected extremity may be pale or cyanotic with diminished pulsations during vasospastic periods followed by swelling, blistering, redness, heat, ecchymosis, possible hemorrhage or gangrene, and possible secondary complications such as lymphangitis, cellulitis, or thrombophlebitis. This condition may be permanent or semipermanent. If a patient is suffering from Buerger's disease or Raynaud's syndrome [diseases involving circulatory defects] should be subjected to the Stahnke treatment, amputation would undoubtedly be necessary."

Shannon concludes "that the 'L-C treatment' of snake-bite should be rejected *in toto*. The use of tight ligatures is not only dangerous but is productive of much more pain than the incisions that Stahnke deplors. Iced water is not only immediately painful but leaves sequelae which may result in amputation or in a permanently physiologically deranged extremity."

This diversity of opinion points to the need for further investigation. Had Stahnke supplied any experimental evidence in support of the treatment he advocates, his conclusions might be more convincing. In view of the rarity of bites by helodermatids, it is unlikely that his method of treatment will be subjected to extensive clinical test. Because many of the smal-

ler laboratory mammals are not so adversely affected by exposure to low temperatures as are human beings, it would be virtually mandatory that tests be carried out with dogs or, preferably, with some of the larger primates.

Shannon (1953b), one of the few members of the medical profession with recent experience in dealing with the bites of helodermatids, notes that the venom is largely neurotoxic, "and judging from the gravity of results seen in bitten laboratory animals it would be well to treat a Gila monster-bite with the same thoroughness as a snake-bite." Unfortunately the effects of neurotoxic venoms are difficult to combat except by means of antivenins, and there is no likelihood that any will become available for helodermatids. In lieu of a specific antivenin, there is little recourse for the physician except to deal with the symptoms as they appear. Antivenins produced for the treatment

of bites inflicted by coral snakes, cobras, or other snakes with venoms that are predominantly neurotoxic might be of some value in treating bites from helodermatids, but there is little reason to expect greatly beneficial results. Aside from the dubious results obtained by Fleisher and Loeb (*in* Loeb *et al.*, 1913) in their tests with cobra antivenin, there is the additional danger of anaphylaxis or "serum sickness," especially in those cases where horse serum has been administered previously.

With our inadequate knowledge of the venom and the meager evidence obtained clinically, there are still numerous uncertainties in the treatment to be recommended for bites by helodermatids. The following suggestions must remain tentative until methods of dealing with the effects of bites by helodermatids have been investigated further.

WHAT TO DO IF BITTEN

Case histories indicate that when a helodermatid engages only the teeth at the front of the mouth, venom may or may not have been introduced into the wound. Because there is no way of ascertaining whether venom has been introduced into the wound until symptoms appear, it is best to assume that it has been and to take measures to remove it. If the lizard has succeeded in engaging the larger teeth at the middle of the jaws, especially the lower jaw, it is virtually certain that some venom is present. On the assumption that a Gila monster or an *escorpión* has seized an extremity, first-aid measures should be taken in the following order:

1. Disengage the jaws as promptly as possible, even at the expense of some laceration. Unless the teeth have been driven into the bone, the victim will have involuntarily withdrawn the hand where the vast majority of bites are inflicted. If the lizard has engaged its larger teeth, removal may require the use of some implement to release the pressure applied by the reptile. The jaws of a pair of pliers, if not too large, can be inserted in the lizard's mouth either in front of or behind the bitten member. Now pull the handles apart, spreading the jaws of the tool as well as those of the lizard. If pliers are not readily available, it may be neces-

sary to use a knife to cut the muscles attached to the jaws. Chisels, crowbars, screw drivers, or similar tools could be used only with difficulty in an effort to pry the jaws apart.

2. If the wounds from the teeth have produced lacerations, incision may not be necessary. If the teeth have been disengaged in such a manner that only punctures are present, a cross incision should be made at each site where a tooth penetrated. Each incision should be approximately as deep as the puncture produced by the individual teeth, perhaps a quarter of an inch if the larger teeth of an adult helodermatid have been driven into their bases. Do not be concerned at the flow of blood; its flow will aid in removing the venom adhering to the sides of the puncture. A razor blade or a sharp knife may be used in making the incisions, preferably sterilized with tincture of iodine, tincture of merthiolate, alcohol, or over the flame of a match. The application of such antiseptics as the tinctures of iodine or merthiolate to the incisions or lacerations may aid in destroying any bacteria carried into the wounds.

3. Apply suction to the lacerations or to the incisions made, using the mouth or any of the mechanical devices supplied with snake-bite or first-aid kits. Suction should be undertaken as soon as possible. If incisions are unnecessary,

apply suction immediately, continuing it for at least half an hour.

4. Apply a tourniquet between the bite and the insertion of the bitten limb, preferably an inch or so from the punctures. The tourniquet need not be tight. Relatively little pressure is required to reduce the circulation. Remove the tourniquet for a few seconds at intervals of 15 minutes.

5. The victim should avoid exertion. There is less danger from shock if he will remain as relaxed as possible, remembering that there is a better chance of removing any venom that may have reached the tissue if the circulation is not accelerated. It should be borne in mind that fatalities from bites by helodermatids are exceptional, and that with prompt application of such first-aid measures as suction, relatively little venom is likely to reach the blood stream.

6. If the victim feels weak or is on the verge of fainting, strong coffee or aromatic spirits of ammonia should be administered.

7. The patient should be carried to a doctor or a hospital as soon as possible, avoiding any exertion en route.

In dealing with the effects of neurotoxic venoms, the physician should place his emphasis on combatting central nervous system symptomatology, according to Shannon (1953b). He recommends the use of such analeptics (drugs with strengthening or restorative effects) as metrazol and picrotoxin, pointing out that the supine position of the patient should be avoided in view of the possible paralysis of the throat musculature and the consequent danger of

mucus obstruction.

In any treatment of bites from Gila monsters or *escorpiones*, it must be recalled that pathogenic organisms are virtually always present in the mouths of these lizards. Consequently it is necessary to take suitable precautions to reduce the danger of infection. Tetanus and gas gangrene antitoxins as well as antibiotics should be administered.

Finally it should be emphasized that bites from helodermatids can easily be avoided, even by those who have legitimate reasons for handling them. The hands need not be used in removing such lizards from cages. Smaller individuals can be seized in stout forceps, while a noose of stout cord, or a forked stick with a cord that draws the lizard's neck up into the crotch, can be used without injury to the reptile. Similar implements can be used in capturing helodermatids. Where it does become necessary to use the hands, while extracting venom for example, there is little danger if reasonable caution is exercised. Interesting though they are, Gila monsters are not to be recommended as pets. So few bites have been reported except from captive lizards that campers, hunters, or others employed in the field within the regions inhabited by helodermatids scarcely need be concerned as long as the lizards are not molested when they are encountered. Not unwisely, the state of Arizona has seen fit to protect the Gila monster (Mulch, 1952), and undoubtedly fewer human beings will fall victim to the bites of these lizards if they are left alone.

MAN AND THE HELODERMATIDS

MYTHS, MISINFORMATION, AND FOLKLORE

ANY VENOMOUS, more or less secretive animal not unjustifiably acquires a sinister reputation. In the imaginations of the human beings that share its habitat it also becomes endowed with outlandish abilities, attributes, or peculiarities. Helodermatids are no exception in this respect, though Jackson (1941) is a bit extravagant in his assertion that no other animal in the United States is "more completely shrouded in ignorance and superstition than the Gila monster." The earliest known account of the *escorpión*, that of Hernández printed in 1615 but actually written prior to 1577 when the manuscript containing it was completed (von Hagen, 1944), is accompanied by a résumé of what would now be termed folklore concerning the animal. Hernández follows his description, evidently based on first-hand knowledge, with a brief account of native beliefs and practices. By means of such phrases as "*sedize*" ("*se dice*" in modern Spanish, for "it is said"), Hernández makes a sharp distinction between what he reports as factual knowledge and what is said or believed by the "*gente*," or people.

The word "folklore" was coined in 1846 to denote the "traditions, customs and superstitions of the uncultured classes in civilized nations" (Encyclopaedia Britannica). Many of the erroneous beliefs concerning helodermatids may, indeed, have their origins among the "uncultured classes," but it will be manifest from the accounts that follow that even the "cultured" have entertained notions that are no less fallacious.

Several of the egregious ideas concerning the Gila monster or the *escorpión* can be attributed to the desire of the ignorant to explain why these lizards are dangerous. As such, they qualify as myths. Other erroneous statements that have appeared in print stem from careless observation, from misguided interpretation, or from a combination of the two. Once an idea becomes fixed in the folklore of a people, it is often embellished or extended to account for other phenomena in addition to the one that it originally was called upon to explain. Or folklore becomes incorporated in tales of adventure, with the narrator as he fabricates his story

adding details, ostensibly from his own experience, that seem to confirm some ancient belief.

Some stories that have appeared in print are little more than yarns, perhaps related with tongue in cheek and intended merely to be amusing. Thus, an article entitled "The Gila monster" published in San Diego, California, in the February 20, 1873, issue of *The World*, relates: "I've seed a lizzard what could outpizen any frog or toad in the world . . . [I] went after it with a stick, but the thunderin' thing, instead of runnin' away like any nateral lizzard, squatted on its tail and spit at me. It were about three feet long, and it had yaller scales all over it, like an alligator's hide, and it were the hardest critter to kill I ever heard tell on. I knocked it over and beat it with a club until my arm ached, but I might as well have tried to cut down a mesquit tree with a blade of grass—the blasted lizzard never stopped spitin'. I jerked out my revolver and fired four shots at it, but the balls all skipped off its tarnal hide back into the river, and, at last I got it so mad I shook the pistol in the critter's face, and I'm a liar if it didn't jump at it and ketch the muzzle in its mouth, and, what's more I couldn't git it away again. I pulled, and jerked, and sweat and swore, but no use; and I believe Mister Lizzard would hev pulled me plum into the river if I hadn't thought to cock the revolver and shoot it down his throat. The shot blew the body clean in two, and then I hope to die if the head and fore legs didn't git the pistol away from me, into the river and swim away with it." (This account, the earliest in which the name Gila monster is used, as far as we have been able to ascertain, was kindly called to our attention by Dr. L. M. Klauber.) While evidently intended to be entertaining rather than informative, this story incorporates many beliefs that were widely entertained in 1873 and that have come down to the present. In a similar vein but with a novel idea Griffith (1955) writes, "In our camp in the Picachos there was a Gila monster who took up residence in a monument and always showed up when he smelled bacon, for a strip of the rind."

In summarizing the various categories of

misinformation, therefore, we have not attempted to distinguish myth from fiction, or folklore from fabrication. Nor is it possible to trace many odd notions concerning the Gila monster or the *escorpión* to their original sources. Some misconceptions have undoubtedly arisen in relatively recent times but may, of course, circulate by word of mouth for several years before they finally appear in print. A few have stemmed from earlier beliefs, fancifully extended, or even from pseudoscientific investigations. Either singly or in various combinations, the habits, abilities, behavior, or morphology of the Gila monster or the *escorpión* are usually involved, but other beliefs include an excessive fear or reverence for one or the other of the species and are properly classified as superstitions. Some of the native beliefs are restricted either to México or to the United States. Others, often with modifications, are common to both countries.

THE BREATH AND ODORS

Stories concerning the breath of helodermatids are among the earliest to appear in print. They have become inextricably interwoven with ideas concerning the odor as well as with the putative spitting abilities of the lizard, and these in turn involve the venom. Sumichrast (1864a, 1864b, 1869) seems to have been the first author to mention the odor in papers that appeared, respectively, in French, English, and Spanish. It is not plain whether he actually refers to the breath of the *escorpión*, but in the English version (1864b), which conforms closely to the versions in French and Spanish, it is stated that "the body of the *Heloderma* usually exhales a strong and nauseous odour, the intensity of which increases at the period when the two sexes seek each other for the purpose of copulation." There may be some truth in this assertion, as helodermatids probably depend upon olfactory cues in locating mates or in other aspects of their courtship. Under some circumstances at least, they do emit a characteristic odor, presumably from the secretions of the paired scent glands in the base of the tail that discharge their contents through the cloacal opening. There is, however, no confirmation for Sumichrast's statement that the intensity increases during the period of mating activity.

Herrera (1895) who probably obtained his information from Sumichrast, makes a similar statement: "*Su cuerpo tiene un olor fuerte y desagradable, más intenso en la época de la reproducción.*" Dugès, in an unpublished manuscript¹ apparently prepared immediately prior to 1899, when he published similar but not identical information, mentions the odor only in connection with the saliva. He observes that a viscous, whitish-colored saliva is produced in some quantity when the *escorpión* bites with fury, and on these occasions one can perceive an odor that is fetid and repugnant ("*en estas ocasiones se percibe un olor fétido y repugnante*"). It is noteworthy in this respect that Van Denburgh (1898) mentions the fetid odor of the venom extracted from *H. suspectum*. Cope (1900), however, seemingly ascribes the odor to the "fetid breath" rather than to the venom of the Gila monster.

The belief that the breath of the Gila monster is not only odorous but actually dangerous seems to have been widely entertained in Arizona at a comparatively early date in the settlement of the region by Americans. Many settlers must have derived their beliefs from the Indians or Mexicans who preceded them.

Bendire (1887) reports that when he was stationed near Tucson, Arizona, in 1872 he had an unusually intelligent Apache Indian attached to his command "who firmly believed that the very breath of the animal was deadly poison, and who could not be induced to go within ten feet of one under any circumstances although it was well known that he was a brave and courageous man on many another occasion." Mention of superstitions concerning the Gila monster were included in the reports of Coues (1875) who mentions the alleged "spiriting of venom" and Yarrow (1875) who had heard the belief that "poison is communicated by the breath." A popular account of the Gila monster by Anonymous (1879) shows how prevalent the belief concerning the breath had become in Arizona, as indicated by information obtained from Mr. T. W. Parker of Phoenix. This gentleman is credited with the statement that when disturbed the Gila monster "stands as

¹ On file in the Herpetological Laboratory, Instituto de Biología, in México City. A portion of the manuscript is reproduced in facsimile by Martín del Campo, 1937.

erect as possible and blows at its antagonist, sending forth a stream resembling fog, and believed by the natives to cause instant death." Anonymous proceeds to relate Mr. Parker's account of a combat between a Gila monster and a snake, after which the snake crawled off "badly hurt." This evoked the comment that "evidently the monster's breath does not paralyze snakes."

The story continues, "A saloon-keeper of his [Parker's] acquaintance captured a monster alive, and kept it for the amusement of his customers. It was tied in a corner, and as the floor was of earth, as in all houses in those parts, the reptile burrowed a considerable hole as a hiding place. One day—Mr. Parker does not say that he witnessed the affair—a mouse ventured near the hole; the monster sent forth a stream of poisoned breath, and the mouse fell paralyzed. The monster then seized and devoured it. One cannot wonder that with so favorable an opportunity no one had the wit to test the truth of the popular belief as to the poisonous character of the monster's breath by submitting to it a variety of small animals."

To do so would, of course, have ruined the story, one that was destined for even greater heights. Colonel A. G. Tassin, in a story said by Garman (1891, quoted by Santesson, 1897) to have appeared in the *Overland Monthly*, evidently believed all that he heard and seemingly added some ideas of his own. According to Tassin, the breath of the Gila monster "in hissing is offensive and issues from a wide-open mouth in puffs of black vapor or smoke. The Mexicans I have questioned all told me that it was exceedingly poisonous, as much so as the bite, if not more, while many of the Americans thought it harmless. Having myself seen a chicken and a small puppy killed by the hissing of one in their faces, I am inclined to think that it is best to keep from coming in contact with it." It is to be doubted that Tassin ever did, or that he ever saw a Gila monster.

In view of the testimony of such reliable witnesses as Colonel Tassin, it is not astonishing perhaps that the following account was re-quoted without comment in the *Homoeopathic Recorder* by Anonymous (1890a) from the *Tucson Daily Citizen* for May 15, 1890: "A few years ago the following well-authenticated fact

occurred in the Huachuca Mtns. A wood cutter who had laid [*sic*] down in complete health to sleep wrapped up in his blanket, failed to arise in the morning when his co-laborers called him. Upon uncovering him, they found him stone dead, and near his body a Gila Monster, which, in the bustle and confusion of the moment made good his escape. As the body of the man bore no marks of a bite or other wounds, we must suppose that his death was caused by the mere exhalation of the lizard."

The assumption concerning the cause of the man's death is quite in keeping with Shufeldt's (1891d) report that "there are a great many people in Arizona and New Mexico, where *Heloderma suspectum* is found, and still more in Old Mexico, where its congener *H. horridum* ranges, that believe that the very breath of these reptiles breathed in a person's face may prove to be poisonous." Anonymous (1890a) quotes a newspaper clipping, ostensibly from a San Francisco, California, paper, which includes a conversation concerning Gila monsters: "It's [*sic*] breath is what kills people. I heard a woman say that a single blast of its breath is sure death."

The belief that the Gila monster's breath could cause the death of other animals evidently was widely circulated, along with living examples of the lizard that were exhibited in parts of the United States (and doubtless elsewhere in the world) far removed from their source. Clarke (1890), prefacing a discussion of the Gila monster's venom, mentions some of the improbable tales concerning the reptile, and expresses his annoyance concerning a story that appeared in a Cincinnati newspaper. According to the news account, the local "zoo" had acquired a Gila monster, which was kept in a cage that was also occupied by a rattlesnake and a copperhead. As recounted by Clarke, "The snakes fell to fighting, each repeatedly striking the other. More than a half column is used in a graphic description of the fight—when Mr. Gila makes his appearance and uses the rest of the column in repeatedly 'opening its jaws and pouring forth a blast of poisonous breath, a poison the most deadly of any animal known to science,' killing the snakes! Of course the snakes died—they killed each other."

Clarke had legitimate doubts concerning the

lethal nature of the lizard's breath, but in view of our present knowledge of the tolerance of crotalids to the venoms of other pit vipers it is equally questionable whether the snakes killed each other. They may have been bitten by the Gila monster with the effects described by Woodbury (1928) and Arrington (1930).

Other accounts mentioning beliefs concerning the potency of the breath include that of Bogert (1930), who writes that "stories are told of Gila monsters with a breath so strong as to turn the grass brown within a radius of six feet." Bogert fails to say so, but this story was circulating in California at the time he wrote and may well have originated as a garbled version of Gadow's (1905) statement concerning a native belief in México. Here the *escorpión*, "when at last secured in a cleft stick, his poison dropping to the ground causes all vegetation to wither for yards around."

The story took other turns. Willey (1906), in a popular account, writes that when angered the Gila monster "emits its breath in a series of quick gasps. The breath is very fetid, and its odor can be detected at some little distance from the lizard. It is supposed that this is one way in which the monster catches the insects and small animals which form a part of its food supply—the foul gas overcoming them." Where other authors had looked upon the foul or fetid breath as a manifestation of innate "cussedness," Willey evidently seeks to account for the nature of the breath in more utilitarian terms. Wright (1906) is inclined to disagree with Willey's supposition and modestly offers an alternate suggestion, "Now, although I do not know much about the Gila monster, it seems to me that a more plausible explanation of the use of this 'foul gas' is that it attracts insects to the lizard, by its resemblance to the odor of putrid meat."¹

¹ A similar notion was expounded by an unknown Jesuit priest writing in 1763. His account, published in a limited edition in 1863, was translated into English and published by the American Catholic Historical Society of Philadelphia in June, 1894, as volume 5, number 2, of their Records. Under what was apparently the original title, "*Rudo Ensayo*," the account was republished in photo-offset printing by Arizona Silhouettes of Tucson, Arizona, in 1951. In the English translation the priest mentions a reptile inhabiting Sonora (which included portions of the present Mexican state of Sonora as well as the southern portion of Arizona),

Little attention was given to Garman's (1891) report, which probably had a limited circulation. He was, however, the first to denounce the belief concerning the disagreeable qualities of the Gila monster's breath and did so in emphatic terms: "The breath is no more colored than that of human beings; neither is it nor could it be any more offensive in its odor than the incense wafted from the lips of multitudes of the representatives of proud humanity. In regard to the breath being venom-laden, that of the specimen before us certainly was not so; here again it would be no very difficult undertaking to select an army of men with whom a comparison in this respect would undoubtedly prove complimentary to the 'monster.'"

Not all subsequent authors have concurred with Garman's belief. Jackson (1941) says that "the breath, while disagreeable and fetid, is certainly no more dangerous than the exhalation from the mouth of any creature that will eat spoiled or rotten food. Part of the halitosis might be traced to the appetite for eggs, no matter how ripe." Dodge (1947) writes that "... although the animal seems to have a chronic case of halitosis, this has nothing to do with its poisonous properties." The same author notes that some persons still insist that "it spits or blows its poison."

The Gila monster does not habitually eat spoiled or rotten food, and Durham (1951) found that rotten eggs were rejected, contrary to the assumptions of Jackson. Carrion is infrequently devoured but could account for obnoxious odors emanating from occasional ex-

writing as follows: "People here call a kind of lizard, which goes on four feet and has a short tail, as if chopped off, a scorpion. It is variously spotted and very poisonous. They say that the only remedy for its bite is to cut off the wounded part immediately. I have seen one as large as a medium-sized cat. It runs very rapidly after its prey, and even attracts [*sic*] it with its infectious breath, catching it at a short distance, like the breyo or boa-constrictor. . . . The Opatas call it *sacara*." As the southern boundary of Sonora at the time the priest wrote was designated as the Yaqui River, it is evident that he was referring to the Gila monster, to which the name "*escorpión*" was applied by Spanish-speaking inhabitants. The name was evidently transferred from *Heloderma horridum*, with which early settlers coming from the south were doubtless acquainted.

amples. Most Gila monsters taken in the field or kept under sanitary conditions in captivity are not particularly odoriferous, although, as do virtually all reptiles, they give off a characteristic scent that most people do not even notice, much less find unpleasant. On the other hand, if one of the lizards has been maltreated or otherwise excited it may have an offensive breath. This can be attributed to regurgitation under stress. As Goodfellow (1907) reported, this may or may not be accidental, but "if irritated it does eject the contents of its stomach, which are more or less fetid, while hanging to an object that it has been exasperated into biting." Hensley's (1949) account of a Gila monster that disgorged nestling rabbits when attacked by a dog offers confirmatory evidence.

Thus Garman's account is subject to modification, but subsequent authors have been incorrect in their assumptions that the breath of the Gila monster is prevailingly offensive. Vorhies (1936) is more nearly right in his assertion that "although reputed to have halitosis so severely that its breath is actually poisonous, this old wives' tale hasn't even a basic item of truth so far as we know."

SPITTING VENOM

Possibly as an inference from the belief (still extant, according to Woodson, 1943a) that helodermatids expel a poisonous spray when they hiss, several authors have quoted informants who believe that such lizards "spit their venom." Sumichrast (1864a, 1864b, 1869) states that when the *escorpión* "is irritated, there escapes from its throat a whitish glutinous liquid secreted by very large salivary glands," but he does not imply that this is forcefully ejected from the mouth. Coues (1875), unconvinced that the lizard is venomous, reports that a belief is prevalent that the Gila monster "has the power of spitting its supposed venom." Werner (1913), quoting the misguided "Captain Spring," states that the Gila monster is also called the "*Escupion*," or "the spitter," a rather fantastic confusion of the name "*escorpión*" so widely used in México for *H. horridum* with the Spanish verb "*escupir*" meaning "to spit." The notion may have been prevalent in Arizona at one time, however, for Brennan (1924) reports that "my uncle also told me that the Mexicans

and Indians called the animal 'the Spitter' and asserted that it spat its poisonous saliva at its enemies." Brennan adds that "this habit has been reported for the Mexican species, *Heloderma horridum* by Ditmars." Barbour (1926) not only also quotes Ditmars concerning the alleged habits of the *escorpión* (which when disturbed, "champed saliva and oozing poison in a foamy froth and then blew it toward the cause of its annoyance in a generous spray"), but is led to make the ill-considered statement that "this habit, so like the poison 'spitting' of some African snakes, is unique among lizards and is a striking example of parallelism in manner of defense." As shown by Bogert (1943a), the cobras that "spit" are equipped with specialized fangs that direct the venom forward in twin jets, aimed with some accuracy at the eyes of an attacker. A small quantity of venom may, indeed, be carried from the mouth of an excited helodermatid when it forcibly expels the air from its lungs, but this is largely fortuitous and can scarcely be construed as spitting. As Dodge (1947) explains, the Gila monster "does not spit poison, but when angered it frequently hisses, the outcoming blast of air sometimes carrying droplets of saliva."

ABSENCE OF AN ANUS

The idea that the Gila monster had no cloacal opening apparently was promulgated to account for the venomous nature of the creature. As recounted in the section dealing with venom, the controversy concerning the presence of venom continued from the time that Cope described the Gila monster in 1869 until after the turn of the century, despite the conclusive experiments of Van Denburgh (1898) and his predecessors. Yarrow's (1888a) disagreement with Mitchell and Reichert, coupled with the support gained from Shufeldt as the arguments continued during the 1890's, undoubtedly had repercussions that continue even down to the present day. As late as 1907 Goodfellow was insisting that the Gila monster "is innocuous *per se*." Seeds of the myth that was later to grow so luxuriously in Arizona were sown by "M" (1907) the same year.

"M" writes: "Old settlers here [in Tucson, Arizona] know of many cases of Gila monster poisoning, in which the effect was death. I be-

lieve that the bite of the Gila monster is dangerous because of the creature's habit of eating lizards, bugs, and rodents, and then lying on the sand so hot that it blisters the hands and feet. The heat causes the food to putrefy in the stomach, evidenced by the fact that the teeth are often covered with a fermented, putrefied froth from the food. A bite has the same effect as the cut of a dissecting knife used on a cadaver; in other words, the inoculation of a deadly poison."

By the early 1930's it was widely believed in Arizona that the bite of the Gila monster was dangerous only because the lizard had no anus; because waste products could not be voided in the usual manner they were expelled through the mouth where they contaminated the teeth. At such places as Grand Canyon National Park, usually in private and never in mixed company, some member of the audience attending the lecture around the campfire would ask the Ranger-Naturalist whether it was true that the Gila monster had no anus; more often the question was couched in much less delicate terms. The myth was already so widely disseminated that it must have originated at least a decade earlier.

By 1936 Vorhies, who had not mentioned the story in an earlier account published in 1917, felt impelled to state, "Heloderma has a digestive tract quite similar to man's—what arrant nonsense to claim that it hasn't." Unaware of the investigation by Rivas (*in* Loeb *et al.*, 1913), who had reported pathogenic organisms in the mouths of Gila monsters, Vorhies was, however, not correct in his belief that "the conception that its mouth is filthy with germs of decay or disease is without reasonable foundation."

Jackson (1941) lists "two common misunderstandings about Gila monsters," one of which "is that the creature has no anal opening, and therefore is poisonous because of the accumulation of decaying waste in the system." Jackson dismisses the belief with the reply that "the reptile has a perfectly normal reptilian alimentary canal." Woodson (1943a) explains that contrary to widespread belief the Gila monster does have a cloaca. Dodge (1947) discusses the myth, and by way of proof for his assertion that the Gila monster has an "anal opening" he reproduces a photograph of the under side of

the lizard's tail to show it. Bogert (1948) as noted by Durham (1951) refuted the belief in reply to a reader of a popular magazine, who wrote, "My friend insists that the poisonous Gila monster, because it eats so little and is so sluggish, has done away with the need of an opening at the lower end of its digestive tract. He says that the creature lives its life without suffering from autointoxication even though it lacks the conventional disposal system. I say that no vertebrate animal has eliminated the need of 'elimination.' Which of us is right?"

Jaeger (1950) states that the myth is prevalent "among cowhands and superstitious people of the country districts," but it is doubtful whether such individuals are any longer more seriously misinformed than those in urban districts. Jaeger himself repeats Sumichrast's absurd assumptions concerning the diet of the *escorpión*, modifying it to read that "the Gila monster's food consists of such things as centipedes and insects." Corle (1951) speaks of "another fallacious theory"—the notion that the Gila monster "has no anal opening and is therefore 'a walking septic tank.'" He believes it to be impossible to say how this idea got abroad, "but it is totally wrong." The same can be said for Corle's belief that the Gila monster will "sit stupidly in the sun for hours without making a motion."

The myth concerning the absence of a cloacal opening in the Gila monster seems to be restricted to the United States, but may well have penetrated the Mexican state of Sonora. In due course the belief will probably be extended to the *escorpión*, *H. horridum* and its subspecies.

"IT STINGS BEHIND"

A belief concerning *H. horridum* that is still widespread in México, to which country it seems to be restricted, was first reported by Sumichrast (1864a). In the English translation of this paper Sumichrast (1864b) states that if the *escorpión* is struck when angry, with the mouth full of glutinous saliva, the lizard "finally throws itself upon its back." This has led the Indians to say that the *escorpión* "must always be attacked in front because it stings behind." Herrera (1895) states the same belief as follows: "Cuando el animal está encolerizado sale de su boca una baba pegajosa y blanquiza

secretada por glándulas salivares muy desarrolladas. Si se le golpea concluye por voltearse patas arriba, y por esto los indios dicen que siempre debe atacarse al Escorpión de frente, porque pica por detrás."

Dugès, in an unpublished manuscript cited earlier in this section, recounts a slightly different version: "*Los indios pretenden que cuando quiere atacar, el reptil se echa hacia atrás sobre su enemigo, de manera que es más seguro agarrarlo de frente.*" Dugès points out that "this erroneous assertion rests on an incomplete observation; when struck from above an escorpión in effect bulges [towards the source of the blow], but it also leans sideways when scratched with some force; when attacked it rushes forward."

The precept, as stated by Sumichrast (1869), "*que siempre se debe atacar al escorpión de frente, porque pica por detrás,*" was heard repeated almost word for word by natives near Chilpancingo, Guerrero, when A. F. Carr and the senior author were searching for *escorpiones* near that city in 1951.

Sumichrast's statement concerning the alleged behavior of the *escorpión* was probably the inspiration for Ditmar's (1910) extravagant description of the gymnastic abilities of the relatively clumsy lizard. Ditmars states: "So agile are some specimens, they can with a jump, entirely reverse their position so the head occupies the spot where the tail had previously rested."

JUMPING

Extraordinary powers of saltation have been attributed to the Gila monster by relatively few authors, most of whom stand by their statements that the animal is slow and lethargic, or that it "waddles away." Corle (1951) exaggerates when he writes that "it can move rapidly, however, when so minded, and it does hiss at an enemy and will spring upon its prey." It is extremely doubtful whether even the most thoroughly infuriated helodermatid can of its own volition leave the ground when it lurches towards an attacker. Were we to believe "M" (1907), however, it would be quite unsafe to venture near a Gila monster. This author cites "an instance of its jumping powers," asserting "I may mention that I once saw some men teasing a Gila monster brought to Tucson. A string was tied around its neck, and a crowd naturally

gathered out of curiosity. The Gila monster was crawling around the ground, trying to get away, but was pulled back by the string. This was carried on till the creature became furious. The crowd around the Gila monster knew nothing of its power to spring. Suddenly he sprang up and bit a man among the crowd on the hand, leaping fully two feet from the ground. The monster was crawling at the time and the string was slack so that it was not jerked in the air." So the writer may have believed, but if the string had not been attached to the animal the lizard would have had more than a little difficulty in reaching an object two feet above the ground. It is possible, of course, that the victim extended his hand, coming closer to the Gila monster than was realized by the observers.

TURNING OVER ON ITS BACK

Like many other assertions presumably but not always explicitly credited to native informants, Sumichrast's statement that the *escorpión* "throws itself on its back" has been widely circulated. When it was finally demonstrated that the venom glands were restricted to the lower jaw (as discussed in the section dealing with the venom apparatus), Sumichrast's assertion was sometimes cited to explain how the venom got into the wound when the lizard was unable to inject it through tubular teeth such as the fangs of cobras or rattlesnakes. As most bites were inflicted by lizards that were right side up at the time, the belief was also called upon to account for the occasional absence of serious effects. The validity of Sumichrast's alleged observation was questioned by Shufeldt (1882, 1890), and Van Denburgh (1897a, 1922) notes that it has not been confirmed. However, as recently as 1935 Hegner writes of the Gila monster that "it is said that it must turn over on its back *before biting* [*italics his*] to allow the force of gravity to carry the venom into the wound." Snow (1906), quoting the redoubtable George Wharton James, was equally gullible.

Arrington (1930) discusses the belief, observing that "some herpetologists contend that little or none of the venomous saliva enters the wound unless the animal turns over on its back. The writer's observations do not agree. The action of the teeth makes a wound that absorbs the buccal secretion quite easily, regardless of

the position of the body. In the case of the baby Gila monster's bite the animal was entirely dorsal side up when the venom was secreted. Quite naturally were the biting reptile on its back, gravity would aid the flow of the submaxillary secretion somewhat, but this is a negligible factor." We agree, as pointed out earlier in this report, for the maxillary teeth may easily pick up venom by capillary action from the pockets in the gum tissue where the venom is expelled from the ducts. In addition, the hissing that accompanies the secretion of the venom in an infuriated helodermatid may assist in carrying the venom to all parts of the mouth.

SNIPPING OUT PIECE OF FLESH

Anyone who has examined the mouth or even the skull of a helodermatid could scarcely fail to observe that the teeth are ill-adapted for cutting. The jaws of helodermatids, like those of most other varanoids, are adapted for grasping (McDowell and Bogert, 1954), rather than for crushing or cutting. But George Wharton James, as quoted by Snow (1906), states that the Gila monster "can bite so quickly that he snips a piece of flesh out easier than one would pinch off a piece of cracker. I have seen this action a hundred times [a likely story!] and this is what one must beware of."

An equally fanciful yarn is recited by "M" (1907): "I may here record still another instance. This of a man whose chief object seems to have been a bravado display of fearlessness. He was holding one of the monsters in his hand by the back of the neck, so it could not bite him. He dropped his hand to the side of his leg. The Gila monster shut his teeth down on his heavy duck overalls, taking a double piece out where the cloth folded, as quick as a pair of scissors could have cut the fabric, and as cleanly."

THE TONGUE AS A STING

The forked tongue of snakes, particularly those known to be venomous, is widely mistaken for the fangs. Or it may be referred to as a sting on the assumption that it is the organ employed by the animal to inject its venom. Because helodermatids are equipped with forked tongues similar to (but far from identical with) those of snakes, it is perhaps inevitable that the tongue has been referred to as a sting. Any-

mous (1890a) quotes a newspaper article that includes the sentence, "A man from Arizona said that the forked tongue [of the Gila monster] was the sting." Shufeldt (1887) saw fit to remark that the tongue was not the dangerous part of the animal. The same author (1890) reports that while the Gila monster walks, "it constantly protrudes, and again whips back into its mouth, its great black tongue, evidently to some degree using the organ as a detector of anything that may possibly stand in the road to impede its progress." Similar beliefs concerning the function of the forked tongue in both snakes and lizards under such conditions were widely accepted, until the work of Kahmann (1932) demonstrated that the tongue was employed to carry odorous particles to the olfactory organs in the roof of the mouth. As such the tongue serves as an auxiliary organ of olfaction.

Jackson (1941) notes that the "wicked looking forked tongue adds to the fear-inspiring picture, although it is completely harmless."

LACK OF IMMUNITY TO THEIR OWN VENOM

It was not until after the turn of the century that it was demonstrated that helodermatids are essentially immune to their own venom. This has most recently been confirmed by Brown and Lowe (1954). An erroneous conclusion to the contrary, however, was reached by Belden (quoted by Anonymous, 1890b), who reported: "A happy family of 6 Gila monsters had been kept in a show case for a couple of months at a prominent store in this city. The animals had eaten heartily and had crawled around as circumstances required; still they slept most of the time and acted sluggishly. One day this case was removed out of doors and placed where the sun's rays poured sharply upon it. Within a short time these animals began to act queerly. They seemed excited and worked themselves in strange convulsive ways. Their tails, which hitherto depended as ornaments, now commenced to thrash, and the animals started upon a quick trot around the cage. As they touched one another they would snap. This was a new feature, as previously they had crawled over one another as over stones and the one trodden upon made no kind of a remonstrance. Soon one monster caught another and bit its legs and feet. A free fight ensued, each one biting and

snapping at anything within reach. Within a few hours from the time of the placing of the cage in the open sunlight all the monsters were dead. Upon careful examination there was no wound of any size to be found, such as should have caused death. There was no severe injury; no loss of blood or any vital fluid whatever. If these animals had not died of poison it would be hard to guess what was the cause of death, and there was no other poison in the cage than that which they contained."

The lizards were, of course, exhibiting the effects of overheating. The convulsive movements preceding their death are characteristic of many lizards exposed to near-lethal temperatures, and in this instance it seems manifest that prolonged exposure to such thermal levels resulted in the death of the Gila monsters.

Gila monsters undoubtedly bask upon occasion, raising the thermal level of the body by such means when it is below the optimum for activity, particularly during the early spring when these reptiles are more often active during the daytime. Air and substratum temperatures are too low to permit them to be active at night until later in the spring and summer. But such statements as Shufeldt's (1890) that they "are fond of basking in the hottest of noonday suns" provide a false impression. Mauldin (1949) was more nearly correct in his statement that "like rattlers, Gilas can't stand the desert sun."

They can withstand exposure to temperatures slightly exceeding 40° C. for brief periods, to be sure, but the reaction of a Gila monster placed in the open on a hot day (when it must be remembered the temperature of the substratum may be well over 38° C., *ca.* 100° F., and often greatly exceeds this level in desert regions) is to seek a retreat as promptly as possible. Arrington (1930) has described the behavior of Gila monsters under such conditions.

This reaction provides the basis, in part, for what Ditmars (1904) first referred to as a "mental change" on the part of Gila monsters placed in the sunlight in the open. Later (1910) he wrote that after a few months in captivity, "when they are the personification of good nature," they can "be handled in the most unceremonious fashion, without the least show of temper." But, "a warm sand bank, in undiluted outdoor sunshine, produces curious psychological phenomena. If left in a place like this for a few

minutes they become different creatures, fiercely snapping from side to side, resenting the least hint of interference with sharp hisses, while they keep their jaws gaping, ready to close upon anything coming within reach."

It seems not to have occurred to Ditmars, or to other authors who make similar assertions evidently derived from one or another of Ditmars's accounts, that the Gila monster becomes active and "excited" under such conditions principally (1) because the absorption of radiant heat raises the thermal level of its body, and (2) because it normally avoids excessive exposure by retreating to the shade. If restrained while attempting to flee, the lizard, stimulated by the rise in its body temperature, is somewhat better prepared to defend itself than it was when kept indoors at subnormal temperatures. Speck (1924), however, interprets the behavior as some mysterious manifestation of "reptile intelligence."

HYBRID ORIGIN

The idea that very distantly related animals are capable of interbreeding seems to have considerable popular appeal. It seems to be a convenient way to explain the existence of animals that seem odd or peculiar or that appear to share the characteristics of two or more other species. Within recent decades, for example, it was claimed by many residents of the Mojave Desert in California that "rattlesnakes had started crossing with gopher snakes." This belief was cited to account for the occurrence of snakes that had no rattle and looked superficially like gopher snakes (*Pituophis*). When such snakes had been examined closely, it was maintained, they proved to have the fangs and presumably other elements of the venom apparatus ordinarily found in rattlers (*Crotalus*). The idea probably stemmed from an examination of a gopher snake, with the forked tongue mistakenly identified as the fangs.

Similar beliefs concerning helodermatids are not widespread, as far as we know, although Garman (1891) and Santesson (1897) both quote Tassin's remarks. Garman writes: "Popular opinion, and for that matter its manner of origin are illustrated by the following, credited to Col. A. G. Tassin, U. S. Army, in the Overland Monthly: 'The Gila monster is an ugly

reptile peculiar to Arizona, and as its name implies, common along the Gila river. It is a sort of cross between a lizard and an alligator."

Whether Tassin was actually attempting to account for the origin of the Gila monster or intended merely to convey an impression of the general appearance of the lizard, it is difficult to say. Hinton (1878) says that a Gila monster taken near Tucson was described as "consisting principally of mouth, having the appearance of an embryo alligator." Whatever Tassin's intention may have been, around the turn of the century it was widely believed that many species were of hybrid origin. In fact the theory was seriously advanced that the major features of evolution could be accounted for in such terms.

The results reported by Griscom Royslott (Cand. Med., 1855, *vide* Klauber, 1948b) in his thesis on "Hybridization on the suborder level," however, show (*vide* Klauber) that helodermatids can be crossed with such distantly related reptiles as cobras. Klauber, who obtained a bibliofilm of the thesis, writes (footnotes in the original have been omitted): "Space does not permit my citing the confirmatory evidence found in the thesis except that the author concludes, in detailing the results of some experiments with the European lizard and the grass snake: 'and the fact that a viable embryo made its appearance would lead to the belief that the hybridization of even such diverse animals as *Heloderma horridum* and *Naia tripudians* [*Naja naja*, the Indian cobra] is by no means impossible. What a creature that would be!'"

This and other pertinent evidence is cited by Klauber in his ingenious explanation of the "discrepancy between Watson's record of a Holmes^[1] statement and what was actually said in *The Adventure of the Speckled Band*." As Klauber observes, "the nature of the creature

that snuffed out the life of Julia Stoner, and, two years later, her unlamented step-father, has long been a puzzle to herpetologists. They have not been satisfied with the accusation levelled at the 'swamp adder, the deadliest snake in India' for, of course, there is no such reptile."

Having delved deeply into the matter, Klauber supplies impressive, authentic, and indisputable evidence. He reaches the inescapable conclusion that Holmes did not say "it is a swamp adder, the deadliest snake in India," as reported by Watson. "On the contrary," Klauber writes, "what he did say was 'it is a *samp-aderm*, the deadliest skink in India,' pointing out in a footnote that the name can easily be translated as 'snake-Gila-monster,' *samp* being the Hindustani word for snake, while the derivation of the suffix *aderm* is plainly from *heloderm*, the vernacular name widely used by European naturalists to refer to the Gila monster and its congener. Thus Holmes, as usual, was being coldly accurate in employing a composite name for a hybrid creature not yet known to science."

Klauber infers that Royslott was able to continue his hybridization experiments in India, where cobras were, of course, easily obtained. If Klauber's surmise is correct, "the gypsies formed the line of communication through which he [Royslott] secured his Mexican specimens." The bastard offspring of the cross is described as "a sinister combination—a creature uniting the intelligence and agility of the lizard with the inimical disposition of the snake. It has fangs in the upper jaw inherited from one parent, and in the lower jaw from the other, and a venom incomparably strengthened by hybridization, thus assuring the almost instant demise of any victim. Here we have an animal that would feed on the batter that was mistaken for milk, for so does its parent, the Gila monster; one with ears like any lizard wherewith to hear a whistle; and one whose legs and claws permitted it to run up a bell-rope as readily as down, especially when it knew there was the warmth of a coal-oil dark lantern awaiting its return to the doctor's room. Here was a reptile that would be handled with a noose on a dog switch; whereas any snake handler would have used a stick terminated with a hook. And, above all, when we combine the cobra and the heloderm the result is certain to assume the likeness of a speckled band."

¹Further evidence bearing on the solution to the problem has been brought to light by Dr. L. M. Klauber since his explanation was published in 1948. With characteristic generosity Dr. Klauber has placed this new information at our disposal. We quote from an enclosure in his letter of May 24, 1955: "It is interesting to note (see *The Adventure of the Sussex Vampire*, par. 6) that Holmes himself commented, while running through the V-volume of his great case-index: 'Venomous lizard or gila. Remarkable case, that!' Thus we have evidence of the importance he ascribed to the lizard phase of the Royslott episode, to which, obviously, he was referring."

"Whether some of the offspring of this foul miscegenation perpetrated by Dr. Roylott ever escaped and became established in the wild is not definitely known," according to Klauber, "but there are three evidences that they did." Two of these are circumstantial, but as Klauber notes, "there are reports of deaths from the bite of an exceedingly active and venomous lizard emanating from an ever widening circle of localities around Ghatal, including Kharar, Khirpai, and even as far west as the Chandrakona. No doubt it was somewhere in this vicinity, not far from Calcutta, that Dr. Roylott maintained his laboratories."

The dispersal of the allopatric hybrid has evidently been rapid, and there can be little doubt that it has many if not all the attributes of a new species. It is sufficiently abundant (displaying the hybrid vigor well known to geneticists) in India to have acquired a common name, "bis-cobra," or "Biskobra," as recently cited by da Fonseca (1949), who mentions it as a "*saurio não identificado da Índia*." Pauloff (1926) has heard rumors of its existence as far north as Manchuria, and the species, for it should now be so considered, must be widely distributed in the Gobi, where, according to Andrews (1937), "all Mongols knew of it."

Andrews (*supra cit.*) states that in the Gobi the creature is known as the "Allergorhaihorhai," and it is believed by the nomads to be "shaped like a sausage and so poisonous that merely to touch it means instant death." There can be no question that the Gobi population was derived from descendants of the hybrids that escaped from Roylott's laboratory in Cal-

cutta, as Andrews himself states that upon learning of the animal he could "only think of the Gila monster."

No scientific name has ever been applied to the creature, but, as we concur with the dictum of Taylor and Smith (1945, p. 128) who state that "all clearly valid species should be made known with a name to systematists,"¹ there seems no alternative but for us to describe it. Plainly a new generic name is needed as well. In recognition of the information supplied by Klauber and by Andrews we propose to call it:

Sampoderma, gen. nov.

DIAGNOSIS: Sausage shaped, with fangs in both upper and lower jaws, those in the upper jaw tubular, those in the lower jaw grooved. Allied to *Naja*, *Heloderma*, and perhaps to the Scincidae as well, for the external morphology is clearly similar to that of some skinks as Klauber (*supra cit.*, p. 156, footnote) observes. *Sampoderma* also has much in common with *Heloderma europaeum* (see H. M. Smith, 1949).

TYPE SPECIES: *Sampoderma allergorhaihorhai*, sp. nov. (fig. 35).

DIAGNOSIS: Sausage shaped; identification of specimens is relatively simple if the following

¹ Mayr, Linsley, and Usinger (1953) in their discussion of allopatric hybridization (p. 37) may also be cited in vindication of our proposal, for they state "The 'hybrid population' may be named as a subspecies [and all rules applying to this category may also be applied to the species, in accordance with the International Rules of Nomenclature] if it satisfies the 75 per cent rule." The population we are describing is 99.44 per cent pure.

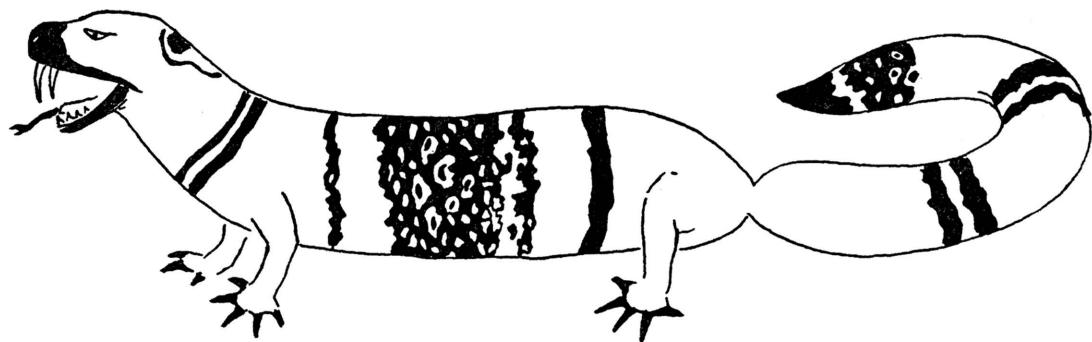


FIG. 35. *Sampoderma allergorhaihorhai* sp. nov. Lateral view of pseudo-ideo-holotype, $\times 1^{10}$. Sex uncertain, presumed to be either male or female. Note vestiges of "spectacle" inherited from the hood of elapid progenitor. Ideogram by Derry Bogert.

procedure is carried out. Touch the specimen, employing the toe, finger, thumb, or, if preferred, the nose. If the result is instant death you may rest assured that you have correctly identified *S. allergorhaihorhai*. Negative results will require that you continue your investigation.

PSEUDO-IDEO-HOLOTYPE¹: Specimen heard of by Mongol in Gobi.

TYPE LOCALITY: Gobi. This may be restricted later when it can be determined which portions of the Gobi the Asiatic Expeditions failed to explore. As no specimens were obtained in the regions visited by these expeditions it is manifest that the species is restricted to other localities.

HYPODigm²: Specimens heard of by Mongols in the Gobi, plus descriptions supplied by Andrews (1937) and Klauber (1948b).

DESCRIPTION: Shaped like a sausage. Venom present. Fangs present in both jaws. Ears present. Legs and claws present. Pattern and coloration like that of a speckled band.

DISTRIBUTION: India, and the regions between the Iron and Bamboo Curtains, and (*vide* Klauber, *supra cit.*) possibly Baker Street in England. The dispersal of the species has been extraordinarily rapid, however, and the species is likely to turn up in any part of the globe.

REMARKS: In this exceptional instance where we have precise information concerning the origin of the species, no question arises concerning the class to which it belongs. The status of neither parental species has been open to question during the last two decades. Bogert (1943a) points out that the spitting proclivities of *Naja naja* do not involve any manipulation of the lips such as would be characteristic of mammals, clearly implying that the affinities of the cobras are to be found elsewhere. Certainly the birds and the cobras are only distantly re-

lated, and we do not hesitate to maintain the position that cobras belong to the Class Reptilia.

As regards the other parental form, McDowell and Bogert (1954) have managed to obfuscate the relationships of virtually all the Squamata, erroneously stating that "Anguinae" should be substituted for the name Anguinae long in use, as Samuel P. Welles (*in litt.*) has pointed out. McDowell and Bogert also shifted the Helodermatidae (and the Helodermidae *auct.*) from the Diploglossa of Camp (1923) to the Platynota of Romer (1945). These authors were unsuccessful, however, in their efforts to prove that the Varanoidea (Platynota of less misanthropic authors) belonged in a separate suborder, as has been conclusively shown to be true of another group, the amphisbaenids, which Smith and Taylor (1950b) refer to the Amphisbaenia of Gray.

Thus, while there is no doubt that *Sampoderma* belongs to the Class Reptilia, it is quite uncertain to which family, much less to which suborder, it should be assigned. There is, therefore, no recourse but for us to propose names for categories between the generic and ordinal levels, which in accordance with the Stenzel System would, of course be: family Sampodermatidae (*not* Sampodermidae, as will be insisted by those who add the family ending to the root rather than to the stem), superfamily Sampodermatoidea, and Suborder Sampodermatomorpha.

We are not motivated by any desire to gain taxonomic fame through the proposal of these higher categories. Were there any way in which we could assign our new species to a suborder currently recognized, we would have followed this alternate procedure.

ERRONEOUS IDENTIFICATIONS

Gila Monsters and *escorpiones*, like other venomous animals, acquire sufficient notoriety that everyone living in the regions inhabited by such animals hears of them and knows that they are dangerous. As helodermatids are partly nocturnal and secretive in their habits, however, not everyone living within the ranges of the two species has actually seen one. There is inevitably some uncertainty concerning the identity of any animal encountered that seems to bear even the remotest resemblance to what is pictured as being a Gila monster or an *escorpión*.

¹ This term is unfortunately omitted from the classification of types by Mayr, Linsley, and Usinger (1953), who quote the absurd statement of Williams that "there can be no possible reason for having any other type except a single one for each name." See also Hubbs (1935, *Copeia*, p. 105), who proposed the term "holo-ideo-duplo-type," carelessly overlooked or perhaps purposely neglected by Mayr, Linsley, and Usinger.

² *Sensu* Simpson, G. G. The reference to the original definition of this term will be found in a footnote in Bogert and Oliver (1945, p. 354).

Furthermore the names of harmless animals are much less likely to be known or to be remembered. In both México and the United States it is not unusual to hear the common names of helodermatids applied to other animals, even in regions far removed from the natural habitats of the venomous lizards.

Shufeldt (1887) notes the "wide circulation of erroneous notions in regard to it [*H. suspectum*], both as to its size, and general appearance; while salamanders, and even 'horned toads' (*Phrynosoma*) and other reptiles all have at various times been pointed out to me as Gila monsters."

Vorhies (1917) writes of the banded gecko (*Coleonyx variegatus*) that "it is feared because it is mistaken for a 'young Gila monster,' this being in part due, possibly, to the light-yellow and dark bands, which, however, are much more regular than on the Gila monster; and to the fact that its small soft scales have somewhat the rounded, bead-like shape of those of the larger animal. (This is assuming that the frightened person looks closely enough to see the scales, which is doubtful.)"

In fact, the frightened person may not even look closely enough to see whether hair or scales are present. On the campus of a university in California (outside the range of *Heloderma*) a professor was lecturing when a spotted skunk (*Spilogale*) wandered into the class room. The professor fled in haste, explaining later that he thought the animal was a Gila monster.

Woodson (1950) relates that "in the Mojave Desert near Daggett a friend dashed up to me and announced, 'I found a Gila monster.' I followed him and it turned out to be a harmless chuckawalla [*Sauromalus*]."

Even in regions as distantly removed as Rocky Mountain National Park in Colorado, the name Gila monster is sufficiently well known to be applied to a salamander. When searching for *Ambystoma tigrinum* in this region, the senior author sought information from the caretaker of one of the hotels, telling the man what some of the characteristics of the *axolotl* were. The caretaker could not recall having seen any creature like the one described, but another member of the hotel's staff said that he had seen an animal that might fit the description of the *axolotl* in a small pond where ice was sometimes obtained on the far side of the valley. His

statement proved to be correct. Several larvae of *A. tigrinum*, including one large specimen, were easily obtained. When the biggest *axolotl*, in a jar of water, with its long feathery gills conspicuous, was shown to the caretaker, his reaction was prompt. "Them?" he asked incredulously, "Hell, I know them. That there's what we call a soft-horned Heely monster."

In México various lizards, particularly anguids, are mistaken for *escorpiones*. Gadow (1905) half a century ago wrote: "At last I thought I had run the beast [*Heloderma horridum*] down, when at Zapotlan in Jalisco. The poison, the sluggish fierceness, difficulty in killing it, all this sounded favorable. We found the *escorpión*, but it was the harmless, gentle *Gerrhonotus*, which for some unaccountable reason is feared as very poisonous."

Some identification of the sort is doubtless the basis for the report of *H. horridum* from the Sierra de Zongolica in Veracruz. Smith and Taylor (1950b) are quite possibly correct in their suggestion that the record is based on *Xenosaurus*.

A sort of double misidentification in reverse was perpetrated by Yarrow (1875) who wrote that "While camped on the Rio Grande near San Ildefonso, N. Mex., in August, 1874, a large lizard presumably of this species [*Heloderma suspectum*], visited the camp, but was not secured, owing to the fact that its sudden appearance frightened the packer, who supposed it to be an alligator." It is anybody's guess what the frightened packer may have seen, as San Ildefonso is far removed from the natural habitats of either the Gila monster or the alligator. Nor could any lizard known from the immediate area be described as large.

PRETERNATURAL POWERS AND ABILITIES

Helodermatids have been credited with attributes that can be described as miraculous, supernatural, or at least as inexplicable. Such beliefs may stem from observations that these lizards are not only dangerous but difficult to kill. As such they may have been looked upon as animals possessing some degree of immortality, despite the fact that many natives have devised ways of killing them, even going out of their way to do so. But fear and respect are so often inherent in religious belief that other powers may have come to be attributed to helodermatids

on the assumption that there was something superhuman or even godly about the animals. In various parts of their range the lizards were or still are regarded as having some influence over such diverse phenomena as the weather, the menstrual cycle, or the fortunes of the people.

Gadow (1905) writes that "in Guerrero and Oaxaca, Colima, and Jalisco everybody speaks of the 'escorpión. He is unkillable unless you crush him with a big stone.'" Somewhat earlier Dugès, in an unpublished manuscript (*supra cit.*) writes: "*Los mismos indígenas dicen también que después de muerto el escorpión es todavía peligroso y no le puede tocar ni con un palo: agregan que si se suspende su cadáver por la cola oscurre del hocico una baba venenosisima, y parece que algo de esto ha valido su nombre de temacuilcahuya pues temalli en mexicano, significa podre. Este punto ser discutido.*" This may be translated as follows: "The same natives also say that after death the *escorpión* is still dangerous and should not be touched, not even with a stick: they add that if the dead body is suspended by its tail a highly venomous saliva trickles from the snout and it appears that something of this sort was the source of the name *temacuilcahuya* since *temalli* in [pre-Conquest] Mexican signified corrupted matter. This is debatable."

A similar belief concerning the Río Fuerte beaded lizard (*Heloderma horridum exasperatum*) is current in southern Sonora, where another element has been added to the belief. Bogert and Oliver (1945) quote John W. Hilton's report that "at Guirocoba the natives fear the *escorpión*, not only for its poison, but as an omen of ill luck. They believe that the only way to break the evil spell caused by encountering one of these lizards is to kill it and hang it up by the tail in front of the house for three days."

In Chiapas, at the southern extremity of the range of the species, the practice of suspending the lizard seems not to be currently in vogue. Thomas McDougall found specimens of *H. h. alvarezi* pinned to the ground with a stake driven through the head. The general practice in Chiapas, as in some other parts of México, is to strike the animal on the head with a machete, a heavy knife that leaves a gaping cut in the skull, usually penetrating the brain.

Superstitions of the sort mentioned by Hilton

and Dugès are not confined to México, for "M" (1907) writing from Tucson, Arizona, asserts that "the Mexicans and Indians after killing a Gila monster always hang it up by the neck on a bush so that it cannot possibly touch its feet, and leave it till it is flyblown or smells before they will trust to its being dead. The creatures apparently are hard to kill or else feign death." Whether a blow on the head stuns a *helodermatid* or induces a state of tonic immobility, attempts to kill Gila monsters or *escorpiones* are not always so successful as their persecutors intend. Woodson (1950) and others have related the experience of a rancher who was bitten by a Gila monster believed to be dead when tied to his saddle.

Woodson (1943b), who may have obtained his information from "M" (*supra cit.*), writes that "Arizona Mexicans and Indians of today, after killing a Gila monster, hang it up by the neck on a bush so that it cannot touch its feet and leave it for days before they will trust to its being dead." If the practice has been continued since January 12, 1952, the Mexicans and Indians would do well to be on the lookout for the game warden. For on that date "The Act Relating to the Protection of Reptiles, Including the Horned Toad and Gila monster" was set forth under "Commission Order No. P-6 in the permanent commission order book of the Arizona Game and Fish Commission" (Grant, 1952). The Act provides that the Gila monster "may be taken only in such a manner as the Commission may prescribe," and it is improbable that the Game Commission will recommend hanging the animal from a bush.

The earliest mention of superstitions concerning the Gila monster rather than the *escorpión* is contained in Coues' (1875) "Synopsis of the reptiles and batrachians of Arizona" wherein it is coyly stated that "females" among the Mexicans of the Territory "have a superstitious belief in the influence of this and some other Saurians may exercise over certain periodical functions of their sex. I am informed by Dr. H. C. Yarrow that in some localities they attribute to *Amblystoma* [*Amblystoma tigrinum*, a salamander] a miraculous power of causing conception—a form of superstition doubtless found convenient at times, especially if shared by their male relatives."

It is also believed that Gila monsters exert

supernatural influences over the elements of the universe, according to Bradford (1895), who reports that "the Indians think they [Gila monsters] produce good or bad weather; they talk to the storm spirit and send wind, water or fire upon us." As recounted by Woodson (1943b), "Certain Indians of Utah avowed that this reptile at will produces good or bad weather; therefore it should not be molested." If accurately reported, the belief represents a practical prescription for the avoidance of a potentially dangerous animal.

Méxican natives attributed remarkable powers of prophylaxis to the *escorpión*. In the Ximénez translation of extracts from Hernández' (1615) work, reprinted in 1888, it is reported that "... *no faltan algunas gentes que se arman, y cubren, con los cueros, deste animal [the escorpión] creyendo que con esto se aseguran, de los animales ponçoñosos, cuya venenossa naturaleza, se embota y reprime con esto.*" Omitting the superfluous commas of the Spanish translation we interpret this: "... some people cover themselves with the skins of this animal, believing that in this way they protect themselves from the bites of poisonous animals, for their venomous nature will thus be weakened and restricted."

Phisalix (1922) prefaces her account of the venom of *Heloderma* with a brief summary of the native beliefs. Concerning *Heloderma horridum* she reports: "*Les Aztèques superstitieux attribuaient à sa morsure la propriété d'engendrer la folie; aussi le trouve-t-on représenté sur la nuque des statuettes d'idiots gâteux, qui constituent quelques-uns de leurs ex-voto.*" [The superstitious Aztecs attributed to its bite the property of engendering madness; also one finds it (the *escorpión*) represented on the nape of statuettes of idiots unable to control their excretory organs, that constitute some of their votive offerings.]

The nature of this belief suggests that the

Aztecs had some knowledge of the effects of the venom. In cases where severe bites are inflicted, such as that reported by Anonymous (1893; quoted in detail in the chapter dealing with the effects of the venom on human beings), serious mental disturbances may accompany other effects produced by the venom. Urination and defecation are also among the symptoms resulting from injections of venom in experimental animals and have been reported for human beings suffering from the effects of *Heloderma* venom. This may explain the symbolism of the statuettes.

Woodson (1943a) claims that "Geologists have discovered stones on which were drawings that depicted men running from angry Gila monsters." That any pictographs of the sort have been authoritatively interpreted we are inclined to doubt. This probably belongs in the same category with the "myths" (Woodson, 1943a) probably perpetrated by showmen that "every letter of the alphabet can be traced on the markings" or that the Navajo Indians have copied some of their designs for blankets from the patterns on Gila monsters. Concerning the latter notion the same author (Woodson, 1950) later says merely that the pattern of the lizard "reminds one of a Navajo blanket." Hylander (1954) makes the somewhat less cautious statement that "the pattern is striking and could be the inspiration for the familiar designs in Navajo blankets."

The Navajos did occasionally venture into the region inhabited by the Gila monster, but their activities were more generally restricted to the plateau north of the deserts. Several Indian tribes, including the Apaches, Pimas, Papagos, Yumas, and Mojaves, shared portions of their lands with the Gila monster, which may have figured in their art. Mr. George M. Bradt of Tucson has shown us a Papago basket evidently intended as a likeness of the Gila monster and readily recognized as such (pl. 20).

VERNACULAR NAMES

Hernández (1615), describing the *escorpión* as a "*cierto genero espantoso de Lagarto,*" was the first author to apply the adjective "frightful" to a helodermatid. Presumably it was his use of the word that led Wiegmann

(1829) to name the Méxican species *horridum*. Since that time such terms as "repulsive," "revolting," or "loathsome" have been applied to the *escorpión* or to the Gila monster, although as Corle (1951) observes, this lizard "is beau-

tiful or not, depending upon your taste." It is not merely a matter of taste, however, for the reputation of the animal inevitably colors the judgment of those who become acquainted with it. An unprejudiced observer, never having heard of the animal, would find it neither loathsome nor repulsive were he to watch it unmolested in its native habitat. But having read or listened to the lurid beliefs, he could scarcely look upon the animal with anything but suspicion. Under such circumstances the animal would not be regarded merely as a lizard able to defend itself effectively, but as a monster that ought to live up to its reputation. This viewpoint is, of course, reflected in the names Gila monster and *escorpión*, both of which have their origins in popular usage.

The common or vernacular names applied to helodermatids have diverse origins. Most of them have been coined by the authors of scientific or popular articles. Others have arisen as a direct result of the need for some way of designating these reptiles in the regions where they are encountered. Vernacular names of this sort may be descriptive or they may reflect ideas or beliefs concerning the animals. Those coined by authors usually attempt to convey some impression of an animal, its attributes, its relationships, its habits, or its habitat or source.

Heloderma horridum: As discussed in the section dealing with the venom and venom apparatus, the application of the name *escorpión* can be traced to European sources, where it was applied to various animals but more especially to those known to be or suspected of being venomous or otherwise dangerous. The name "scorpion" now generally used in English to designate the arthropod equipped with a sting at the posterior end of the body was doubtless derived from either the Latin or Greek. But it cannot be safely inferred that either *scorpio* or *skorprios* was originally used solely to designate the animal we now refer to in English as the scorpion.

Whatever its original source, *escorpión* was established among the Spanish-speaking inhabitants of México (or Nueva España) as the name for the venomous lizard by the time Hernández (1615) had completed his manuscript in 1577. Hernández also recorded the Aztec name "*Caltepepon*," or "*Acaltepepon*" (rendered as

"*Acastelpon*" by Phisalix, 1922). The Nahuatl name "*Themacuicahuya*" (also written *Temacuicahuya* or *Temacuicahuilla*) was also mentioned by Hernández. While Werner (1913) gives "*Tola-Chini*" as the Aztec name, and Gadow (1905) states that the Zapotecan name for the species is "*Talachini*," this name is actually of uncertain origin. Mr. Paul Rütthling, in field notes on file at the American Museum, records the Zapotecan name obtained from natives in Tehuantepec in 1920 as "*Guchachigishe*," which he translates as "iguana-hammock,—because the markings resemble the mesh of a hammock." Pawlowsky (1926) mentions the name "*Silafica*" as one employed by the Mexican creoles, but we have not ascertained the original source, or its significance.

In German the name "*Krustenechse*" is more often used, dating from Schinz and Brodtmann (1833). Duméril, Bibron, and Duméril [1836 (1834-1854)] used the name "*L'Heloderme hérissé*," but modern French authors have usually referred to the species as "*l'Heloderme*," or "*l'Heloderme granuleux*" (Angel, 1942). Woodson (1950) mistakenly says that "natives call it 'El Scorpion.'" As Werner (1913) mentions, the name "*Escorpión*" is based on an erroneous assumption explained elsewhere in this report. Ditmars (1907) apparently coined the name "Mexican beaded lizard," and the name "Beaded Monster of Mexico" has also been used (Jackson, 1941). In order to distinguish the three subspecies of *H. horridum*, we have suggested herein the following names: Río Fuerte Beaded Lizard, or *Escorpión del Río Fuerte*, for *H. h. exasperatum*, and Chiapan Beaded Lizard, or *Escorpión Negro*, for *H. h. alvarezi*. This leaves the names Mexican Beaded Lizard, or *Escorpión*, to be applied to the nominate race, or to the species as a whole.

Heloderma suspectum: The name "Gila monster" probably became established in Arizona shortly after Americans began to pour into the region at the conclusion of the Mexican War in 1846. However, Bartlett (1854), the Boundary Commissioner whose party surveyed the region between 1851 and 1853, crossing what is now Granite Pass in the Peloncillo Mountains of New Mexico, later traversing most of the valley of the Gila River, does not mention the name. A collector, Dr. Thomas H.

Webb, accompanied Bartlett's party, but there is no evidence that he obtained any Gila monsters. The type specimen figured by Baird and erroneously labeled *H. horridum*, only five years after Bartlett's account appeared, was obtained by Schott while he was attached to the Emory Survey, which followed Bartlett's.

In his "Personal narrative," Bartlett often mentions the Indians, in which he was particularly interested. But he says virtually nothing of importance about the animals encountered. There are casual references to "hundreds of rattlesnakes," one of which bit a mule, and towards the end of his account he says: "But while the parched desert plains are so destitute of quadrupeds and birds, they abound in reptiles and insects in the greatest variety. Lizards of every size and color, from one and a half to eighteen inches in length are found here; all of which are harmless." No other lizard except the Gila monster in Arizona attains a length of 18 inches, although chuckawallas (*Sauromalus*) approach these dimensions. But his statement that the lizards were all harmless suggests that he may not have seen the secretive Gila monster. Any Indian in the Gila Valley undoubtedly could have informed him that it was venomous, but, as similar beliefs were doubtless entertained concerning other lizards, Bartlett would not of necessity have been impressed by such information concerning the Gila monster, even were it certain that he had seen one.

Within two decades after Bartlett's visit, however, the name must have come into general use in Arizona. Possibly it was first mentioned elsewhere,¹ but the earliest printed references to the lizard's name that we have found appear in the reports of Coues and Yarrow, published in the same volume in 1875. Coues speaks of the "Gila monster," as this large and repulsive reptile is called," and Yarrow mentions "this reptile, called 'Gila monster' by western settlers." Previously Cooper (1869) had coined the name "Warty Lizard" for the species, still listed as *H. horridum*, however, as Cope's application of

the name *suspectum* appeared the same year.

Lockington (1879) also spoke of the Gila monster, and the same year the second popular article so titled was published (Anonymous, 1879). In the United States it has been almost universally called Gila monster ever since. Elsewhere it has been referred to as the "Arizona Poisonous Lizard" (Flower, 1937), "the Sonoran heloderm" (Anonymous, 1882a), or by German authors as the "*Gilatier*," "*Gila-Echse*" (Werner, 1913), or as "*Schauderechse*" (Kohlhaas, 1941). Angel (1942) calls it the "*Gila monstrueux* or *Lézard venimeux d'l'Arizona*." Similarly the English name has sometimes been translated into Spanish as "*Monstruo de Gila*" (Cuesta Terrón, 1930, 1934), or into Portuguese as "*Monstro de Gila*" (da Fonseca, 1949). In this report we have suggested the names Reticulate Gila Monster for the nominate subspecies, and Banded Gila Monster for *H. s. cinctum*, in order to distinguish the two races when referring to them in the vernacular.

Viquez (1935, second edition not dated, ca. 1940), in a somewhat confused account titled "*El Perro Zompopo*, (*Lagartija venenosa*)," but illustrated with a dubious figure of *H. suspectum*, suggests that some sort of venomous lizard may occur in Costa Rica. He implies that it is related to the "*Monstruo de Gila*," but no fatalities are known in Costa Rica from its bite. In the second edition it is "*Perro Zompopo*," modified from "*Perro Sompopo*" in the first edition. The name is quite possibly applied in Costa Rica to some lizard, *Gerrhonotus* or perhaps *Lepidophyma*, that is believed to eat ants, as the name "*zompopo*" widely applied to the umbrella ant implies. It may be noted, incidentally, that a gecko (*Coleonyx mitratus*), known in Costa Rica as "*El Escorpión Tobobo*," is widely suspected of being venomous.

According to Barnes (1935), the name Gila "appears to be of Indian origin, meaning 'spider,'" but opinions expressed by other authors leave some doubt. Barnes quotes Hodge's statement that "the name Gila, or Xila, was apparently originally that of an Apache settlement west of Socorro. As early as 1630 was applied to those Apaches residing part of the time on headwaters of Gila river."

¹ Dr. L. M. Klauber has called our attention to an article with the title "The Gila monster" that appeared in *The World* (vol. 2, no. 179, p. 1), published in San Diego, California, on February 20, 1873.

UTILIZATION OF HELODERMATIDS

AS MEDICINE

As is well known, folk remedies employed in various parts of the world often include the administration or application of portions of animals. Reptiles are not infrequently used. The earliest description of a lizard's hemipenis was based on a dried specimen obtained in a market in India where it was probably sold as an aphrodisiac. Similar beliefs concerning the efficacy of helodermatids as drugs have been entertained in México, where the meat was employed, and in the United States, where the homeopaths sought to use the venom.

Hernández (1615), in Ximénez' translation of his account of the *escorpión* (as noted by Martín del Campo, 1936), reports, "*la carne de los lomos, deste animal, comida en pesso de dos ouolos, que hazen vn escrupulo, sedize que despierta el apetito venereo, admirablemente, de manera que en esto no reconoce ventaja á otro qualquiera medicamento, para el efecto.*" This may be translated: "The meat of the loins of this animal, eaten in the weight of two ovulos, which equals one escrupulo [1.198 milligrams], is said to awaken the sexual appetite better than any other known medicament." We do not know how widespread this belief may have been in México, nor whether it is still held. It is at variance with Sumichrast's (1864b) report that "I have been told of a great number of cases in which ill effects were produced . . . by eating its flesh in mistake for that of the Iguana."

In the section dealing with the venom and venom apparatus, we have mentioned the efforts of the homeopathic practitioners to make use of the toxic saliva of *Heloderma* as a drug. Charles D. Belden, a practitioner living in Phoenix, Arizona, appears to have been the first doctor to suggest its use. His letters, quoted by Anonymous (1890a), mention that the Gila monster, which the homeopaths persisted in calling *Heloderma horridus*, "does not bite frequently, but when it does it is understood that the result is a benumbing paralysis like to *paralysis agitans* or to *locomotor ataxia*. There is no tetanic phase." Belden concludes his letter with an inquiry concerning means of obtaining the poison and preserving it.

A second letter in the same article relates Belden's difficulties in shipping a Gila monster,

which neither the express company nor the post office would accept alive for shipment. Being resourceful, he himself extracted venom from three of the lizards obtained in Phoenix. Holding a watch glass between the jaws, he succeeded in obtaining "a few drops of pasty yellowish fluid. It quickly dried up on the glass. I sprinkled sugar of milk upon it to absorb it, and with a clean steel I removed it from the glass into two small vials, one containing alcohol, 95%, the other sugar of milk."

Two years later Boocock undertook the task of "proving" the venom. His detailed and astonishingly frank account published the following year (Boocock, 1893a, 1893b) tells in detail how this was done. "Boericke and Tafel sent me a vial of the 6x trituration. Of this I dissolved one drachm vial in four ounces of diluted alcohol, and after succussing for half an hour, I medicated with this some No. 35 globules, and took three or four drops, or wet my finger while I was succussing. I . . . was seized with such an internal coldness from my heart, as if I was being frozen to death internally, and I had no way of warming myself. Resisting the temptation to take something, because I believed that this was the direct result of the drops of *Heloderma horridus* I had licked from my fingers, I resolved to bear it as well as I possibly could. But, oh, the coldness from within outward! My mind was clear, and movements were good as usual; nothing but internal coldness, as if I was filled with a deathly coldness.

"I wrote to Dr. T. F. Allen to ascertain if he knew of any antidote; he did not know of any, and I believe not any is known. After suffering for some time until supper was ready, I ate some hot sour pickles, which warmed me some, and I think antidoted the poison. *Acetic acid* may be an antidote to this alkaline poison. At least it is worth remembering. Oh, how powerful this new poison!"

After consulting with Dr. Allen, Boocock concluded that the "6x trituration" dosage was too strong, and it was decided that the "30th potency" was "low enough to prove." Noting that the venom was said to be alkaline and that death is remarkably sudden from its effects and said to be the result of paralysis of the

heart, Boocock proceeds to report the result of his "proving." "My notes are to be jotted down as I am about my professional duties, and as feelings are noticed."

Before listing what he had jotted down in the way of feelings and symptoms, which required over a score of pages to cover not only the first but a second "proving," Boocock describes himself as of December 5, 1892. "I am in my sixtieth year, sanguine, billious temperament, fair complexion and weigh 160 pounds, height 5 feet 6 inches . . . I am in very good health. Good appetite, sleep well, dreamless, awake about 4 a.m. to urinate, and then sleep until 6 a.m., when I get up for the day. By this afternoon's mail received from Boericke and Tafel *Heloderma horridus* 30th. At once took one drop on my tongue, one hour and a half after lunch. Good feeling. . . ."

Nothing is reported for the intervening days, but on December 9, "I had already taken one drop of the 30th, with a severe nervous headache, but I forgot that I took the medicine. I have medicated 2 oz. No. 35 globules with 30th dilution, and have taken six globules as a dose before they were dry."

The time of day when the original notes were recorded is occasionally indicated, although dates are mentioned only sporadically. Or at times the author records what happened on a previous day, as when he writes, "Last night whilst retiring had some sharp, shooting pains in my bowels, more on the left side of the abdomen, and sharp twinging in left testicle. During the night had some erection of penis, but felt too tired to take advantage. A feeling of great prostration. In my dream this feeling of weakness was uppermost; I was in my dream delivering a temperance lecture, and would have made this weakness an excuse, but remembered that I never make excuses when in any way I am able to go; so delivered my lecture, but had this strange feeling as if I was asleep, or was perfectly unconscious of what I was saying, and only became conscious when I had finished, at the applause."

Many of the supposed effects from the highly diluted venom reappeared from time to time, and apparently no "symptom," however unimportant it might seem, was omitted from Boocock's account. The doctor evidently regarded the venom as a "medicine," even while he was

"proving" it, for early in his account he states: "No medicine taken to-day. My head felt sore all the day, with aching at the base of the brain; very weak; no desire nor inclination for exertion in any way. Heart has a good deal of sticking pain, shooting through towards the right side from left. Stitches in the abdomen, followed by a loose, copious stool, lumpy, of good color. Urine scanty. Trembling a good deal in my left side, hands very shaky. The ringing of my office-bell would startle me into a trembling. Am very weak, very nervous. No headache, but a sore feeling. Mind clear. Calm feeling. A desire to be quiet. Copulation long and very enjoyable. A large flow of semen."

These excerpts will suffice to show the nature of Boocock's report. He was careful to mention at intervals that his mind was clear, doubtless wanting it made plain that mental disturbances had not interfered with his judgment in reporting the results of the tests that he had carried out on himself.

At the conclusion of the report on his third "proving," Boocock (1893b) on February 12, 1893, adds that "copying my notes has brought so vividly to my memory that I can almost feel the cold arctic rays through my body, and the giddiness and staggering gait of the *Heloderma hor.* days. I hope that you may have many others more courageous than I have been, whose provings will compare or improve upon this poor effort of mine."

Under the heading "Clinical" he appends a report on his uses of the "medicine." A patient "whose staggering gait was called to my mind by my feelings, is now taking *Heloderma hor.* c.c., twice daily, and is steadily improving." Another patient with chorea "who has suffered with blue cold hands since I cured him of paralysis. . . . has been taking *Heloderma hor.* c.c. four times daily for a week, and is now able to be up and about. . . ."

The following year Boocock (1894a) wrote to Boericke and Tafel, inquiring whether they had "any higher dilution or trituration of *Heloderma horridus* than the 200th." He also wanted to know "how many are using or studying it. As I think I may safely call it my own discovery, I am anxious to look after it somewhat. I am a poor man, and perhaps it is only through something like this that I may be able to make my mark on the generation in which I have lived,

and so, perhaps perpetuate my name. I have some ambition in this direction. . . . If king and queen of the world could offer millions for a moment of time, then I have in this a means of arresting death on its flight in heart failure and paralysis of lungs. What else will come from it God only knows." The editors of the journal in which the letter was published add in brackets that "*Heloderma hor.* may be had in the 30th, 100th, 200th or 500th dilution."

In a second communication published the same year, Boocock (1894b) elaborates on his letter, stating among other things that he is repeatedly asking himself: "What is heart failure? What is paralysis of the lungs? And am so far compelled to believe that these are caused by a paralysis of the great sympathetic nervous system or the various motor nerves. But I must not say any more about these, for I know very little about them. . . . Would it not be wonderful if it is found through some such drug proving as this that all the diseases, mental and physical, are caused by some of the finer nerves, nerves too fine for the most powerful microscope to see under post-mortem examination. . . . All this kind of thinking has been caused by the effects of *Heloderma horridus*, my proving of it and experience with it."

Boocock continues his account, describing a patient suffering "from erysipelas and dropsy in the legs. . . . [who] appeared to be sinking. . . . Pulse, fifty, temperature, ninety, and to all human appearance was rapidly dying; all said so, and I fully believed so, but left *Heloderma* [*sic*] *horridus*, one powder in water, and ordered her tongue to be moistened with a feather dipped [*sic*] in this every half hour." Boocock was waiting to be "notified of her death, but no such notice coming called, and to my surprise, found everything changed. I then gave *Hela. hor.* 200 every two hours, with placebos. All the bad symptoms gradually disappeared."

Anonymous (1894b) adds a confirmatory note: "The publication of the schema of Dr. Boocock's proving of *Heloderma hor.* in this issue reminds us of a little incident in connection with this proving that is not without interest. Quite a number of those who read the proving shrugged their shoulders and cried [quite understandably, it seems to us] 'too sensational.'" Anonymous then relates how a young clerk employed by Boericke and Tafel "laughed at the

whole thing, and in a spirit of bravado began to take the remedy, six doses in all, of medicated pellets of the 6th potency. On the second night he awoke, and the first impression that flashed through his mind was that he was under the influence of the *Heloderma*, and it was not a pleasant sensation by any means. He felt a cold sensation creeping down his body and legs, and was in a *very* cold and clammy sweat . . . by morning the disagreeable experience began to pass off and he felt no more of it." The author warns against giving "this remedy" too frequently "else there may be serious and unlooked for aggravations. . . . It is suggested as a remedy for paralysis agitans and might be found useful in any chronic abnormal movements of any part of the body. It might also be thought of for people with cold, fishlike hands. It certainly is an interesting remedy, and one that when understood may occupy a very important place."

Boocock was also supported by Dr. Charles E. Johnson, quoted by Anonymous (1894a) earlier the same year. Johnson, writing from Denison, Texas, wanted it known that a case, "pronounced incurable by many physicians," who had many of the symptoms developed in Boocock's provings, including "that awful coldness," had been given "two doses of the 200th." The patient was delighted with the result for the coldness nearly disappeared, leaving a comfortable glow.

The year 1894 was evidently an important year for Boocock, for aside from the support obtained by Anonymous, who was presumably the editor of the *Homoeopathic Recorder*, the results of his "provings" were "arranged" by Lilienthal (1894) of San Francisco. Lilienthal managed to condense in four and a half pages all that Boocock had reported, listing the symptoms under such headings as "mind, head, eyes, ears, nose, face, mouth, throat, stomach, hypochondria ('gurgling in region of spleen' is mentioned under this heading), abdomen, stool, urinary organs, sexual organs, respiratory organs," and so on, winding up with "generalities" as a category for any symptoms reported by Boocock that did not seem to fit elsewhere.

Boocock's earlier hope that he would make his mark on the generation in which he lived was being borne out. It must have been a source of gratification to the courageous doctor when

Bradford (1895) the following year mentioned Boocock's provings, reporting that "it would seem that in *Heloderma* we have a valuable remedy for certain forms of paralysis. In an incurable case of hemiplegia the 30th of *Heloderma* was given in water, a teaspoonful every 3 hours. The patient took but a few spoonfuls, as she said it made her feel badly and she stopped taking it. She complained of a sensation of the most intense coldness in the paralyzed side. She died within a couple of days."

Bradford was undaunted by his patient's death, however, for he concludes that "the sensation of coldness, attributed to no known cause, may be the keynote of this remedy, which may become, after further provings [Boocock may have raised his eyebrows upon reading this!] and experience, a second *lachesis*." The latter name was applied to another venom, that of the bushmaster (*Lachesis mutus*), used in homeopathic practice in treating such different ailments as septicemia, varicose veins, peritonitis, and diphtheria. Apparently it had been in use for several years before Boocock achieved fame through his proving of "*Heloderma horridus*."

Interest in this "remedy" did not wane despite Bradford's failure to keep his patient alive. In 1898 Cameron again "arranged" (or perhaps "rearranged" would be more appropriate in view of Lilienthal's previous efforts) the symptoms that Boocock had reported as the result of his provings. Cameron credits Belden with securing the venom of the poisonous lizard. He also endeavors to correct the name that had been applied to the drug, using the name *Heloderma horridum* in the title of his article, followed by "*Suspectum*" in parentheses. Subtitles include "Gila Monster" and "Lacertidae," with the latter name evidently intended to denote the family to which Cameron thought the lizard belonged. He prefaces his arrangement with some citations from "Clinical Authorities," listing the reports of Boocock, Johnson, and that of a Dr. E. E. Case, who had evidently employed the drug in treating locomotor ataxia. (We have not seen Case's report, published in Medical Advance for July, 1897.)

Cameron employs much the same categories as those listed by Lilienthal, but manages to include more detail so that his "schema" is about twice as long. In part the greater length

reflects the inclusion of some odds and ends of information, mostly from the pen of Capt. John A. Spring, including Spring's story of the miner who succumbed "to what in Germany is called the galloping consumption," after being bitten by a Gila monster. This account is listed by Cameron under the category, "Stages of Life."

But the influence of Boocock's discoveries must have been on the decline after the turn of the century. We have found no references to the use of the venom as a drug since Cameron's account appeared, although homeopathic physicians may possibly have continued to use it, at least until the supply of Gila monster venom obtained by Belden in 1890 was exhausted. The homeopathic literature was generally ignored by allopathic practitioners, as well as by such scientific investigators as Loeb (*in* Loeb *et al.*, 1913). While Pawlowsky (1927) cites some reports that appeared in homeopathic journals, it is uncertain that he ever saw them. Phisalix erroneously cites Belden, whose letters were quoted by Anonymous (1890a, 1890b), but she specifically states that she had been unable to procure the journal containing his account. Not having read this, Phisalix gratuitously inferred that Belden had attempted to carry out immunization experiments with the venom of *H. horridum*.

Viewed in the light of present-day knowledge, the ideas of the homeopaths at the time that Boocock (*supra cit.*) wrote seem on a par with those entertained by the natives in México during the sixteenth century when Hernández was preparing his account. Cooke and Loeb (*in* Loeb *et al.*, 1913) found that venom injected directly into the stomach or intestine of a guinea pig produced no discernible symptoms, although it was uncertain whether the venom was destroyed by the digestive juices or absorbed by the contents of the digestive tract. From these results it may be questioned whether the venom would have any physiological effects if taken internally. Symptoms supposedly produced by Boocock's ingesting the venom in such minute quantities, or the beneficial effects reported to have been produced in patients to which "*Heloderma hor.*" was administered, would now be explained in psychosomatic terms. For that matter some of the "symptoms" that Boocock included in the re-

ports of his "provings" would be considered more or less normal in a person of his age and temperament. There might even be a faint suspicion that Boocock was boasting in reporting some of the supposed effects from the "medicine" he was taking. It seems doubtful, but perhaps he had read what Hernández wrote about the indigenous beliefs in México.

Loeb and his colleagues (*in* Loeb *et al.*, 1913) made extensive use of the venom of *Heloderma* in their investigations, which were carried out with the avowed intention of learning something of theoretical rather than of practical value. No effort was made to find therapeutic uses for the venom; though they attempted to produce an antivenin experimentally, they did so solely for theoretical reasons and not with the intention of providing a remedy for the venom of *Heloderma*. Phisalix (1922) carried out immunization experiments with the venom of the Gila monster for similar reasons.

Various investigators have sought to find therapeutic uses for snake venoms (Bogert, 1943b, provides a popular summary), theorizing that neurotoxic elements inhibiting nerve action might be employed as analgesics, or that coagulants present in some venoms might be used in treating hemorrhage. No investigations of the sort have been made with the venom of *Heloderma*. Mulch (1952), however, makes the ambiguous statement that "studies now being conducted in Dr. Stahnke's laboratory [The Poisonous Animals Research Laboratory, at Arizona State College in Tempe, Arizona] are of definite therapeutic value, and may some day aid medical authorities in combating cancer and other human diseases." The results of such studies, presumably of the therapeutic uses to which the venom of *Heloderma* might be put, have not been published.

COMMERCIAL VALUE

The hides of the Gila monster and the *escorpión* have rarely been used for leather. The presence of osteoderms in the skin precludes the possibility of tanning it satisfactorily, quite aside from the fact that neither species of *Heloderma* is sufficiently abundant to be commercially important in this respect. Mounted skins, usually more aptly described as stuffed,

have had a limited market. A dealer in Phoenix, Arizona, offered them for sale in 1930 at prices varying from \$5 to \$7.50 apiece.

The principal demand for helodermatids comes from zoological gardens, museums, roadside "zoos," sideshows, and circuses, where the animals have frequently been exhibited. *Heloderma horridum* is imported into the United States from México for distribution by dealers, mostly in Texas. Arizona has been the principal source of supply for *Heloderma suspectum*. Tradesmen supplying them usually sell other animals, as well as cacti, or other desert products. Arrington in 1930 commented that "it appears to have no real economic value," but the same year a dealer in Phoenix offered Gila monsters at prices ranging from \$2.50 to \$7, "according to size." More recently Mulch (1952) reports, "Commercial outfits were paying 25 to 50 cents an inch . . . and selling them to out of state dealers for a dollar to two dollars an inch. With a price ranging from between 20 and 40 dollars on his head, Mr. Gila monster was headed for disaster."

An article in the Arizona Republic of Phoenix under the date June 23, 1924, was headlined, "Enterprising Phoenician sees big future in Gila monster business so is establishing reptile gardens." The account states that a local dealer has "a selection of 200 of them for you, all alive and happy and fat, and in any size you wish. . . . He is equipped to do business with the person seeking a collection as well as he who just wants a monster, say, for a pet." The account concludes with the exaggerated statement that "Homesteaders, prospectors, roadbuilders and health seekers have sold several thousand dollars' worth of the reptiles and the demand is increasing steadily."

It is doubtful whether any statistics are available concerning the traffic in helodermatids, although Kohlhaas (1941) claims that dealers in Germany were importing Gila monsters in moderate quantities and shipping them to various parts of the world, with some of the specimens resold to zoological gardens or educational institutions in the eastern parts of the United States. Mauldin (1949) mentions the unfounded rumor in Arizona that a "zoo in the East had once paid four thousand dollars for a twenty-three inch" specimen.

IS THE GILA MONSTER NEARING EXTINCTION?

Within a decade after Cope (1869) supplied the name *suspectum* for the Gila monster, fear was expressed that the lizard was destined for oblivion. Lockington (1879) pronounced his belief that the slow-moving lizard, with peculiarities that "render it easy to be captured . . . will ere long become extinct, as it is killed wherever found." Shufeldt (1891d) over half a century ago was also worried, for "collectors are now rendering it scarce over nearly all of its range, and no doubt the time is not far distant, comparatively, when this highly interesting species will meet with utter extinction." Only four years previously, however, Bendire (1887) had asserted that it "was not rare around Tucson," and 45 years later, despite the depredations of collectors, dealers, and the casual killing of Gila monsters by local inhabitants, King (1932) expressed the opinion that "the Gila monster is still quite common in the foothills of the ranges surrounding Tucson."

But anxiety concerning the fate of the Gila monster continued to be expressed or implied in various accounts. Arrington (1930), pointing out that "it is strictly a poisonous reptile, but its habits prevent it from being a real menace," asserts "in a great many ways the lizard is truly a peculiarity, and . . . there are many who advocate its preservation." Woodson (1943a) concurs, restating the belief of Lockington and Shufeldt that "there is a possibility that some day the Gila monster will become extinct," and adding that "this can be prevented if lovers of desert life will make it a practice to tell their friends that the Gila monster, after all, is a 'monster' in name only."

As noted earlier in this section, a law has been passed in the state of Arizona to protect the Gila monster. Grant (1952) reports this as "probably the first legislation to protect a poisonous animal," and mentions that a \$25 fine had been imposed on an individual who had either killed a Gila monster or had one in his possession. Carr (1952), in a caption to a picture illustrating an article dealing with the founding of the Arizona-Sonora Desert Museum, notes that the Gila monster, now protected by state law, "is becoming scarce" and that the animal will be exhibited "with a label explaining that it 'minds its own business.'"

Mülch (1952) sought to explain and defend the law protecting Gila monsters shortly after it was passed, citing his belief that "roadside zoos and reptile gardens . . . were rapidly reducing their numbers." By way of evidence for his conviction he reports: "Since 1939 Dr. Stahnke has taken advance herpetology students into the field twice yearly, once in the spring, and once in the fall, to collect specimens throughout the Salt River Valley. It was not uncommon for students to capture two or three specimens on a trip. By 1947 the scientist became acutely aware that the Gila monster was beginning to disappear from the scene, and that former hunting areas in the valley were no longer producing specimens."

This can scarcely be construed as valid reason for believing that the Gila monster has become seriously reduced in numbers. As Jackson (1941) observes, "at best the reptile is not numerous." The number seen abroad in any region fluctuates, not only seasonally but from year to year, probably as a result of numerous factors of which the amount of rainfall during the warmer months is possibly the most important. There can be no question that collectors or those who needlessly kill Gila monsters, either purposely or by accidentally hitting them on the highway while driving motor vehicles, have had some effect upon the population. But as late as 1953 the lizards were still to be found within the city limits of Tucson, a city with a population that has been expanding for well over a century, having had a human population of 1000 even prior to 1850 (Bartlett, 1854). The city now has a population of over 50,000, not all of whom have had encounters with the Gila monster. But there can scarcely be an inhabitant who has not seen one.

It would seem, therefore, that the secretive habits and cryptic coloration of the Gila monster provide it with sufficient protection to enable it to resist rather effectively such enemies as human beings. The statements of Lockington and Shufeldt, like the statement of Mülch, do not so much reflect the actual scarcity of Gila monsters as they do the abilities of the lizard to escape detection. Destruction of normal habitats in Arizona by overgrazing, truck farming, and in recent years the planting of

cotton may have been a more important factor in any decrease in the number of Gila monsters in Arizona than collectors. While these lizards do occasionally occur in such places as alfalfa fields, the clearing and plowing of the land can scarcely have anything but an adverse effect upon them. Still there are many areas left within the range of *H. suspectum* where habitats have not been seriously disturbed, particularly in the rocky foothills where the Gila monster is most often found.

While the needless killing of Gila monsters should be discouraged, and some regulation of the traffic in these reptiles is probably desirable, it is little short of ridiculous to make it difficult, if not impossible, for legitimate educational institutions to obtain specimens for exhibition or study. At the time that Grant (1952) wrote, only one permit had been issued. It was supplied to a man said to be "conducting research using the venom of the gila monster."

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