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JIMMY A. McGUIRE

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Cover illustration: An adult male *Crotaphytus dickersonae* photographed approximately 2 km north of Bahia Kino Nuevo, Sonora, Mexico (see Fig. 31B).

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ABSTRACT

A revision of the alpha taxonomy of Crotaphytidae revealed that there are at least 12 and probably 13 species. A data set including 88 characters drawn from osteology, squamation, soft tissues, color pattern, life history, and behavior was collected. In addition, an allozyme data set composed of ten phylogenetically informative characters was obtained from the literature. Analysis of these data resulted in the following hypothesis of relationships: ((*Gambelia silus* (*G. corona*† (*G. copei* + *G. wislizenii*))) + (*Crotaphytus reticulatus* (*C. collaris* (*C. antiquus* (*C. nebrius* (*C. dickersonae* (*C. grismeri* (*C. bicinctores* (*C. insularis* + *C. vestigium*))))))))). Although little character evidence in support of crotaphytid monophyly has been presented in the literature (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989), crotaphytid monophyly was found to be strongly supported with five fixed, unambiguous synapomorphies. Strong support was also discovered for monophyly of *Crotaphytus* (12 fixed, unambiguous synapomorphies) and *Gambelia* (six fixed, unambiguous synapomorphies). The hypothesis of relationships estimated here was used to address life history and morphological evolution within the group including the relationship between head morphology and diet, the evolution of display-oriented morphology in males, the evolution of bipedal locomotion, and a functional consideration of gravid coloration. A taxonomic account is provided for Crotaphytidae, *Crotaphytus*, *Gambelia*, and each species. Each species account includes a synonymy, an etymology, a diagnosis for the species, a detailed description of scalation and coloration, a section describing maximum adult size as well as size dimorphism, a description of the species geographic distribution with a dot distribution map, an account of the known fossil record, a summary of available natural history information, and a listing of references that provide illustrations of the species. Separate dichotomous keys are provided for males, females, and juveniles of *Crotaphytus* and *Gambelia*.

INTRODUCTION

Lizards of the family Crotaphytidae (collared and leopard lizards) are among the most familiar squamates of western North America. This familiarity probably stems from their relatively large size (compared to other North American lizards), often vibrant coloration, predatory lifestyle, and pugnacious habits. Crotaphytidae, one of nine iguanian families proposed by Frost and Etheridge (1989), is currently comprised of two genera, *Crotaphytus* (seven or eight species) and *Gambelia* (three species), that range from southern Idaho in the northwestern United States, southward into southern Baja California and northern Mexico, and eastward into the states of Missouri, Arkansas, and Louisiana. They have been the subject of numerous studies of ecology, physiology, reproduction, hybridization, and historical biogeography, and many of these studies have addressed questions of a historical nature (e.g., Savage, 1960; Montanucci, 1970; Ingram and Tanner, 1971; Axtell, 1972; Smith and Tanner, 1974; Montanucci et al., 1975; Tanner and Banta, 1977; Tanner, 1978; Sanborn and Loomis, 1979; Tollestrup, 1979, 1983; Murphy, 1983; Welsh, 1988). However, despite several important systematic analyses of the group (Smith and Tanner, 1972, 1974; Montanucci et al., 1975), phylogenetic relationships within Crotaphytidae remain largely unresolved. Although the monophyly of the group has never been questioned, few derived characters have yet been offered to support this contention (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). The same can be said for the monophyly of the genera. The phylogenetic relationships of the group have been addressed using cladistic methodology only once (Montanucci et al., 1975), and that study predated important methodological advances in cladistics, such as outgroup analysis (Watrous and Wheeler, 1981; Maddison et al., 1984).

There are three primary goals of the present study. The first goal is to revise the alpha taxonomy of Crotaphytidae in order to provide a better understanding of species diversity within the group as well as an appropriate selection of terminal taxa for phylogenetic analysis. The second goal is to provide an estimate of the phylogenetic relationships of Crotaphytidae. The third goal is to use this phylogeny to investigate morphological and life history evolution among crotaphytids and provide a taxonomy that is logically consistent with the evolutionary history of the group.

HISTORICAL REVIEW

The earliest accounts of crotaphytid lizards were closely associated with the joint military–scientific exploratory expeditions of the American frontier. In fact, it was only shortly after the epic Lewis and Clark expedition of 1803–1806 that the first crotaphytid species was described. As a member of a party headed by Major Stephen H. Long that was exploring the Great Plains, Thomas Say collected and later described *Agama collaris* (James, 1823). *Agama collaris* was later placed as the sole member of the newly erected genus *Crotaphytus* by Holbrook (1842) in his classic account of the North American herpetofauna.

A second crotaphytid species, *Crotaphytus wislizenii,* was obtained at Santa Fe (New Mexico) by Dr. Wislizenus, an army surgeon, who made the collection during the Mexican–American War of 1846–1848. This species was first described by Baird and Girard (1852*a*), and a more detailed description was given by the authors (1852*c*) shortly thereafter in Stansbury (1852). From their first formal descriptions, crotaphytid lizards have been thought to form a natural group, despite the difficulty that more recent students have had in discovering synapomorphies.

In August of the same year, Baird and Girard (1852*b*) described two additional species of *Crotaphytus*: *C. dorsalis* from the desert of Colorado, and *C. gambelii,* for which locality data was lacking, although it was thought to have been collected in California. In December, Hallowell (1852) described a fourth species, *C. fasciatus* (a junior synonym of *G. wislizenii*), from the sand hills at the lower end of Jornada del Muerte, New Mexico. Hallowell's specimens were part of Samuel Woodhouse's collections made during the early 1850s, again emphasizing the important role that the early expeditions of the American West played in crotaphytid taxonomy. In 1854, Hallowell proposed the genus *Dipsosaurus* for *C. dorsalis.*

Duméril (1856) transferred *Crotaphytus collaris* to the genus *Leiosaurus,* a decision that was very likely influenced by the similarity in head morphology and squamation in these genera. Furthermore, Duméril (1856) suggested that *C. fasciatus* Hallowell was synonymous with *Leiosaurus fasciatus* Duméril and Bibron 1837 (= *Pristidactylus fasciatus* fide Etheridge and Williams, 1985). However, he provided the substitute name *L. hallowellii* to be used in the event that they were not found to be the same species. This taxonomy was not addressed by North American herpetologists until Cope (1900).

Baird (1858) described *Crotaphytus reticulatus* based on specimens collected by J. H. Clark and A. C. B. Schott of the Mexican Boundary Survey. Baird designated syntypes (both labeled as USNM 2692) taken from Ringgold Barracks, Texas (Fort Ringgold Military Reservation, Starr County). In his description, Baird (1858), without comment, erected the subgenus *Gambelia* for *Crotaphytus wislizenii.*

Yarrow (1882*b*) described *Crotaphytus copeii* from La Paz, California (Baja California Sur, Mexico), based on a specimen collected by L. Belding.

Stejneger (1890) described *Crotaphytus baileyi* from the Painted Desert, Little Colorado River, Arizona. This western form was recognized on the basis of two rows of interorbital scales, compared with the single row found in *C. collaris,* as well as smaller supraoculars, and a narrower head with a longer snout. He did not believe that *C. baileyi* warranted more than subspecific recognition; however, no intergradation zone was known at the time, and following the rules of the American Ornithologist's Union, he felt obligated to describe the form as a distinct species. Stejneger (1890) also described *Crotaphytus silus* from the San Joaquin valley of California.

In 1899, Mocquard described *Crotaphytus fasciatus* from Cerro Las Palmas, Baja California. It is clear from his description and the accompanying figure that this is a juvenile specimen of what is now referred to as *Crotaphytus vestigium,* and, as the name *fasciatus* predates that of *vestigium* by 73 years, the former name has priority (see the *C. vestigium* taxonomic account for an assessment of the nomenclatorial implications of this taxonomy).

Cope (1900) resolved several long-standing taxonomic problems within *Crotaphytus* when he synonymized *C. gambelii, C. fasciatus* (Hallowell), and *Leiosaurus hallowellii* (= *C. fasciatus*), with *C. wislizenii.* He also synonymized *C. copeii* and *C. silus* with *C. wislizenii,* citing an absence or gradation of distinguishing morphological features. Citing the work of Stejneger (1890), Cope did not support the recognition of *Crotaphytus baileyi* at either the specific or subspecific rank. Over the next 50 years, there would be considerable disagreement with respect to the proper taxonomic ranking of *baileyi,* with some authors recognizing *baileyi* as a subspecies of *C. collaris,* others as a distinct species, and still others choosing not to recognize it at any taxonomic level.

Mocquard (1903), apparently realizing that the name *Crotaphytus fasciatus* had already been applied to a leopard lizard species by Hallowell (1852), provided a substitute name (*C. fasciolatus*) for the Baja California species. However, Cope (1900) had already synonymized *C. fasciatus* Hallowell with *C. wislizenii.* Thus, *C. fasciatus* Mocquard remained the senior synonym for the Baja California species of collared lizard.

Stone and Rehn (1903), noting a series of 11 specimens collected in the Pecos region of Texas that displayed the diagnostic characteristics of both *C. collaris* and *C. baileyi,* recognized the western populations as a subspecies of *C. collaris, Crotaphytes* (sic) *collaris baileyi.* Meek (1905), citing the constancy with which the supraorbital semicircles were unfused in the specimens he examined from Baja California, California, Arizona, and Utah, again followed Stejneger (1890) in recognizing *Crotaphytus baileyi* at the specific level. Over the following few years the taxonomic rank of *baileyi* jumped back and forth between the species and subspecies level. Ruthven (1907) followed Stone and Rehn (1903) in recognizing *baileyi* as a subspecies. After 1907, the taxonomy of *baileyi* more or less stabilized, with most workers recognizing this form as a subspecies of *C. collaris.*

Van Denburgh and Slevin (1921) provided a brief description of *Crotaphytus insularis* from Isla Angel de La Guarda in the Gulf of California, Mexico. Van Denburgh (1922) could find no differences between *C. copeii* from Islas de Cerros (= Cedros) and Magdalena and *C. wislizenii,* and following Cope (1900), recognized only the latter. Also, Van Denburgh (1922) incorrectly synonymized both *C. fasciatus* Mocquard and *C. fasciolatus* Mocquard with *C. wislizenii.*

In 1922, Schmidt described *Crotaphytus dickersonae* from Isla Tiburon in the Gulf of California, Mexico. In the description, he correctly hypothesized that the species might be found on the adjacent Sonoran mainland as well. Schmidt agreed with Van Denburgh (1922) in not recognizing *C. copeii,* citing extreme variation in the color pattern of this species throughout its range. Burt (1928*b*) synonymized *Crotaphytus collaris baileyi* with *C. c. collaris* on the basis of extensive variation in the interorbital scale characteristics used to separate the two forms, a taxonomy that was not followed by subsequent workers. Allen (1933) reduced *Crotaphytus dickersonae* to a subspecies of *C. collaris*, citing intergradation in the hindlimb and tail length characters that Schmidt (1922) used to distinguish *C. dickersonae* from *C. c. baileyi*. Allen (1933) did not follow Burt's (1928*b*) synonymy of *C. c. baileyi* with *C. c. collaris*.

Mittleman (1942) discussed the higher level phylogenetic relationships within North American iguanian lizards. His diagrammatic representation of relationships placed *Crotaphytus* as the sister taxon of *Petrosaurus* and *Streptosaurus*. This group was in turn depicted as the sister group of the phrynosomatid sand lizards *Uma, Callisaurus*, and *Holbrookia*. Despite the relationships implied by his tree, he appears to have considered *Crotaphytus* to be a relatively primitive iguanid (*senso lato*), because he suggested that the sand lizards were derived from *Crotaphytus*-like stock, as was *Sauromalus*.

Smith (1946) separated *Crotaphytus wislizenii* from *C. collaris* and *C. reticulatus* by placing it in the genus *Gambelia*, thus elevating Baird's (1858) subgenus to generic rank. This controversial decision initiated much debate among various workers on the group. Furthermore, Smith (1946) reduced *G. silus* to a subspecies of *G. wislizenii*. With respect to higher taxonomic relationships within the Iguania, Smith followed Mittleman (1942) in placing *Crotaphytus* and *Gambelia* as the sister group of *Streptosaurus* plus *Petrosaurus*, and this group as the sister taxon of the phrynosomatid sand lizards. Smith and Taylor (1950) elevated *dickersonae* from a subspecies of *Crotaphytus collaris* to the rank of full species.

Fitch and Tanner (1951), reinterpreting the data of Burt (1928*b*), recognized *Crotaphytus collaris baileyi* as a subspecies distinct from *C. c. collaris*. This taxonomy had generally been followed in the literature despite the earlier synonymy of the two by Burt (1928*b*). In addition, they described a new subspecies of *Crotaphytus, C. c. auriceps*, from the upper Colorado River basin.

Returning to the higher-level relationships within the Iguania, Savage (1958) presented a phylogeny that differed radically from that of Mittleman (1942) and Smith (1946). In his classification, Savage proposed a new subgrouping, the iguanines, that included *Crotaphytus* plus those genera later placed in the Iguanidae by Frost and Etheridge (1989).

Cochran (1961) recognized *Crotaphytus silus* as a full species. Robison and Tanner (1962) attempted to resolve the *Crotaphytus–Gambelia* debate by examining osteological and myological evidence. As a result, they chose not to recognize *Gambelia* as a genus distinct from *Crotaphytus*.

Tanner and Banta (1963), in the first of a three-part series examining the systematics of leopard lizards, described a new subspecies, *Crotaphytus wislizeni punctatus*, from the upper Colorado River basin of Utah and Colorado. Like Cochran (1961), those authors did not recognize the genus *Gambelia*.

Etheridge (1964) removed *Crotaphytus* from Savage's (1958) iguanines because he was unable to find any character or combination of characters that would serve to diagnose the iguanines if *Crotaphytus* was included. Furthermore, he hypothesized that *Crotaphytus* may be the sister taxon to the sceloporines (= Phrynosomatidae) plus tropidurines (= Tropiduridae).

Leviton and Banta (1964) resurrected the name *copei* for the Baja California populations of *Crotaphytus wislizenii*, recognizing *C. w. copei*.

Weiner and Smith (1965) attempted to resolve the *Gambelia–Crotaphytus* controversy by examining the osteology of the group. They placed all members of *Crotaphytus* (including those that had been placed in the genus *Gambelia*) into a grouping they referred to as the "crotaphytiform" lizards. They recognized only four species of crotaphytiform lizards: *C. collaris, C. reticulatus, C. insularis*, and *C. wislizeni* (again relegating *silus* to a subspecies of *C. wislizeni*). Thus, without presenting evidence, Weiner and Smith (1965) reduced *C. dickersonae* to the rank of subspecies within *C. collaris*. Those members of the genus with a superficial resemblance to *C. collaris* (*C. collaris, C. reticulatus*, and *C. insularis*) were further separated into the "collariform" group. Finally, with respect to the *Gambelia–Crotaphytus* debate, they concluded that the subgeneric rankings, *Crotaphytus* (*Gambelia*) *wislizeni* first proposed by Baird (1858) and *Crotaphytus* (*Crotaphytus*) were the lowest levels of taxonomic segregation that could be justified by the data.

Soulé and Sloan (1966) followed Weiner and Smith (1965) in recognizing *dickersonae* as a subspecies of *C. collaris* and reduced *insularis* to a subspecies of *C. collaris* as well.

Banta and Tanner (1968), in their second study of leopard lizard systematics, provided a redescription of *Crotaphytus wislizeni copei* and described a new subspecies, *C. w. neseotes*, from Isla de Cedros off the west coast of Mexico. They did not follow Weiner and Smith (1965) with regard to the subgeneric groupings.

In response to Weiner and Smith (1965), Montanucci (1969) entered the *Gambelia–Crotaphytus* debate. Based on an examination of the osteology of *C. wislizenii, C. silus, C. collaris*, and *C. reticulatus*, he concluded that there should be no generic or subgeneric segregation within the group. He also recognized *C. silus* as a species distinct from *C. wislizenii*, based on unpublished data. *Crotaphytus dickersonae* and *C. insularis* were again recognized as full species distinct from *C. collaris*. In a paper published the following year, Montanucci (1970) formally elevated *Crotaphytus silus* from a subspecies of *C. wislizenii* to a full species based on morphological, ecological, and behavioral differences.

Ingram and Tanner (1971) described *Crotaphytus collaris fuscus* from the Chihuahuan Desert region. The subspecies could not be diagnosed by discrete morphological characters and was proposed on the basis of a distinctive discriminant function.

In 1972, Holman described *Crotaphytus oligocenicus* on the basis of a right dentary from the early Oligocene Cypress Hills Formation, Saskatchewan, Canada.

Smith and Tanner (1972) were the first to recognize that there were additional distinct *Crotaphytus* taxa occurring primarily west of the Colorado River. They described *Crotaphytus collaris bicinctores* from the Great Basin region and *C. insularis vestigium* from the peninsular ranges of Baja California, Mexico, and southern California. Using a Ward's Minimum Variance Cluster Analysis, they found that there were two phenotypically distinct groups of collared lizards (excluding *C. reticulatus*), each comprised of four named forms. The "western complex" was found to include *C. i. insularis, C. i. vestigium, C. c. bicinctores*, and *C. c. dickersonae*, while the "*collaris* complex" was found to include *C. c. collaris, C. c. baileyi, C. c. auriceps*, and *C. c. fuscus*. Despite these findings, they described *bicinctores* as a subspecies of *C. collaris* and chose to recognize *C. dickersonae* as a subspecies of *C. collaris*, as well. Thus, their own classification did not follow the phylogenetic relationships they had proposed.

Axtell (1972) considered *Crotaphytus collaris bicinctores* and *C. c. baileyi* to be distinct at the species level based on morphological differences and a narrow hybrid zone between the two in the Cerbat Mountains of Arizona. He tentatively placed *bicinctores* as a subspecies of *C. insularis*.

Smith and Tanner (1974) again recognized *bicinctores* as a subspecies of *Crotaphytus collaris*. They based this taxonomic decision on intergrade specimens between *C. bicinctores* and *C. collaris* in northwestern Sonora, Mexico, and southwestern Arizona, as well as the hybrid specimens identified by Axtell (1972) from the Cerbat Mountains of Arizona. However, the presumed intergrade specimens were actually *C. c. nebrius*, subsequently described by Axtell and Montanucci (1977), with the characteristic features of this species. They substantiated their previous recognition of *C. dickersonae* as a subspecies of *C. collaris* on the basis of intergrades between *dickersonae* and *collaris* from the Guaymas region. However, these specimens are again *C. nebrius*. Based on the results of their cluster, canonical, and discriminant function analyses, they provided two potential phylogenetic hypotheses for *Crotaphytus* shown here in parenthetical form: (*wislizenii* (*reticulatus* + ((*fuscus* (*collaris* (*baileyi* + *auriceps*))) + ((*dickersonae* + *bicinctores*) + (*insularis* + *vestigium*))))) or (*wislizenii* (*reticulatus* + ((*insularis* + *vestigium*) + ((*dickersonae* + *bicinctores*) + (*fuscus* (*collaris* (*baileyi* + *auriceps*))))))). These hypotheses of relationship differ in that the first recognizes a group that includes *C. c. dickersonae, C. c. bicinctores, C. i. insularis*, and *C. i. vestigium*, while the second recognizes all of the *C. collaris* subspecies as a group. In addition, Smith and Tanner (1974) again recognized *silus* as a subspecies of *C. wislizenii*.

Montanucci et al. (1975) made the first attempt at a cladistic analysis of the group. As a result of their electrophoretic study, they recommended the recognition of *Gambelia* as a valid genus, elevated *Crotaphytus wislizeni silus* and *C. collaris dickersonae* to full specific status, and removed *C. c. bicinctores* from *C. collaris* (again recognizing *C. i. bicinctores*). They did not recognize *C. c. auriceps*, considering it to be a junior synonym of *C. c. baileyi*. They found the character states present in *C. dickersonae* to be confounding and proposed a possible hybrid origin for the species. Their proposed phylogeny of the group was similar to those of Smith and Tanner (1972, 1974), except that *C. dickersonae* was included with Smith and Tanner's (1972) "*collaris*-complex." The soon-to-be-described *C. c. nebrius* (included as *C. collaris* ssp.) was also included in this complex. Their data suggested the following phylogenetic relationships: ((*bicinctores* (*insularis* +

vestigium)) + (*reticulatus* (*dickersonae* (*collaris* ssp. (*c. collaris* (*c. fuscus* + *c. baileyi*)))))).

Axtell and Montanucci (1977) described the new subspecies of *Crotaphytus collaris, C. c. nebrius,* from the Sonoran Desert of southeastern Arizona and Sonora, Mexico. In the same year, Tanner and Banta (1977) published the third paper in their three-part study of the systematics of leopard lizards. They did not follow Montanucci et al. (1975) in recognizing *Gambelia* as a valid genus, or Montanucci (1970) in recognizing *G. silus* as a species distinct from *G. wislizeni.* In addition, they described a new subspecies, *Crotaphytus wislizeni maculosus,* from the Lahontan basin of western Nevada and parts of northeastern California, southern Oregon, and the Snake River basin of southwestern Idaho.

Montanucci (1978) again recognized the genus *Gambelia* and the species *G. silus* as valid taxa, while he synonymized the subspecies *G. w. neseotes* from Isla de Cedros with *G. w. copei* of the adjacent Baja California peninsula.

Sanborn and Loomis (1979) elevated *Crotaphytus insularis bicinctores* to full specific status on the basis of distribution, squamation, and male display pattern differences.

Wyles (1980) studied albumin immunological distances between *Gambelia wislizenii* and the remaining crotaphytine species recognized by Montanucci et al. (1975). Wyles (1980) concluded that the immunological distance estimates were well within the range observed for other iguanid (*sensu lato*) genera and thus recommended that *Gambelia* again be reduced to a subgenus.

Smith and Brodie (1982) erected the subfamily Crotaphytinae for *Crotaphytus* and *Gambelia,* thus providing the first higher taxonomic name for the group.

Montanucci (1983), citing relative phenotypic similarity between *bicinctores* and *vestigium* and discounting the significance of the behavioral differences proposed by Sanborn and Loomis (1979), again recognized *bicinctores* as a subspecies of *Crotaphytus insularis.* Estes (1983) synonymized *Gambelia* with *Crotaphytus.* This taxonomic decision evidently passed unnoticed by most neoherpetologists and was not followed by later authors. In any event, Cooper (1984) and all later authors have referred to *Gambelia* as a valid taxon.

Etheridge and de Queiroz (1988) were the first to provide evidence that the Crotaphytinae formed a monophyletic group, which they referred to under the informal heading "crotaphytines." However, they were unable to find any uniquely derived character states for the group and hypothesized its monophyly based on a unique combination of derived yet homoplastic character states.

Frost and Etheridge (1989) reaffirmed the findings of Etheridge and de Queiroz (1988), although they also were unable to find any unique derived characters for the group. They elevated the subfamily Crotaphytinae of Smith and Brodie (1982) to familial status, recognizing Crotaphytidae as one of nine monophyletic iguanian families.

Norell (1989) described an extinct species of *Gambelia, G. corona*†, from the Pliocene–Pleistocene boundary of the Anza-Borrego Desert, California.

Collins (1991), citing the evolutionary species concept of Frost and Hillis (1990), elevated *C. i. vestigium* (and, consequently, *C. i. insularis*) to full species, although no evidence was presented indicating morphological or genetic differentiation between the two taxa. McGuire (1991), in a note summarizing a geographic range extension, again recognized *vestigium* (and thus *insularis*) as a subspecies of *Crotaphytus insularis.*

MATERIALS AND METHODS

The characters used in this study were obtained primarily from the skeleton, squamation, and color pattern, with additional characters taken from the hemipenes, behavior, and life history (hereafter referred to as the "morphology" data set). The allozyme data set of Montanucci et al. (1975) also was reanalyzed. A few specimens were cleared and stained using the method of Dingerkus and Uhler (1977). Most external anatomical characters were scored from formalin-preserved specimens stored in alcohol, although some color pattern characters (noted in the character descriptions) could be observed only on live animals or in photographs of live individuals (field observations were made on all crotaphytid taxa and photographs taken of all crotaphytid taxa except *Gambelia silus*). Characters were scored primarily from adults, although some juveniles were included when ontogenetic variation was not evident in the characters in question. Unless otherwise stated, scale terminology follows Smith (1946), skull terminology follows Oelrich (1956), and postcranial skeletal terminology follows Etheridge (1964, 1965, 1967), Hofstetter and Gasc (1969), and de Queiroz (1987). Museum numbers of crotaphytid specimens examined and their localities are listed in Appendix 1, along with museum numbers of iguanian outgroup taxa examined.

Hypotheses of phylogenetic relationships were estimated using cladistic analysis (e.g., Hennig, 1966; Wiley, 1981). Character states were polarized using outgroup analysis (Watrous and Wheeler, 1981; Maddison et al., 1984), a procedure that was complicated by the lack of interfamilial resolution within Iguania (see discussion of outgroup taxa below). Many characters could not be polarized unequivocally and these were described as "unpolarized" or "not polarized" in the character descriptions. Once character polarities were obtained, a hypothetical ancestor was constructed summarizing the hypothesized ancestral states for each character. The hypothetical ancestor was included in the analysis in order to root the tree. The phylogenetic software employed here was a test version of PAUP (version 4.0.0d26, Swofford, 1995). Because the number of taxa is relatively small, the branch-and-bound algorithm of Hendy and Penny (1982) was employed, guaranteeing that all most parsimonious trees would be discovered. Logical incongruencies (e.g., transformations of the collar pattern in species that have no collar) were coded as missing or unknown data ("?"). Following the recovery of the most parsimonious tree, tree stability and phylogenetic information content were tested using the nonparametric bootstrap (Felsenstein, 1985; 2000 bootstrap replicates), as well as analyses of tree length distribution skewness (g_1 statistic; Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992) and the decay index (Donoghue et al., 1992). Simulations indicate that a strongly left-skewed distribution of tree lengths (described by a negative g_1 value) is an indicator of phylogenetic information content of the data (Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). Hillis and Huelsenbeck (1992) provided critical g_1 values for data matrices composed of various numbers of binary and four state characters. Because this data set differs from the simulated data sets generated by Hillis and Huelsenbeck (1992) both in number of characters and in the numbers of states per character, new g_1 critical values were calculated that are specific to this data set using a computer program written by J. Huelsenbeck (Table 1). These values were generated by randomly reshuffling character states among taxa in the original data set 100 times and recalculating the g_1 for each reshuffled matrix. Critical values at both 95 percent and 99 percent confidence intervals were then calculated from the distribution of g_1 values generated.

Table 1.—*Recalculated* g_1 *critical values expected for random data for the morphology-only, allozyme-only, and morphology + allozyme (allozymes coded using Manhattan distance frequency approach) data sets and the observed* g_1 *value for each.*

	Number of informative characters	Number of taxa	$P = 0.05$	$P = 0.01$	Observed
Morphology only:	88	13	−0.15	−0.16	−1.49
Allozymes:	10	7	−0.43	−0.45	−0.50
Morphology + Allozymes:	98	13	−0.15	−0.15	−1.45

FREQUENCY CODING

The character coding scheme applied to morphological data in this analysis is a frequency approach developed by Wiens (1993*b*, 1995). An approach wherein polymorphic characters are excluded from the analysis is rejected because it is clear that many characters will be found to be polymorphic given a sufficient sample size. This was especially evident in this analysis as large sample sizes were available for both preserved (up to 87 specimens per taxon) and osteological (as many as 55 specimens per taxon) material. Under the frequency approach, each binary character is partitioned into 25 bins (a–y), each representing 4 percent of the total range of possible frequencies that may be observed in a polymorphic or monomorphic character (i.e., bin a = 0–3%, bin b = 4–7%, and so on; Table 2). Note that it is necessary for one of the bins to have a range of 5 percent rather than 4 percent in order to encompass the entire range of possible frequencies (0–100%); this bin was arbitrarily chosen as bin y (96–100%). Twenty-five frequency bins were used because this was the maximum number of whole number bins (i.e., 4 percent vs. 3.26 percent per bin, etc.) that PAUP is able to include (although PAUP will allow up to 31 bins; Swofford, 1995). Those characters that were analyzed using frequency coding were treated as ordered, following the assumption that any character state transformation must pass through a polymorphic state, no matter how transitory, before reaching fixation (Wiens, 1993*b*, 1995). Frequency coding was not applied to the three mul-

Table 2.—*Frequency values for the 25 ordered bins employed in the frequency coding analyses (Wiens, 1995).*

a =	0–3.99
b =	4–7.99
c =	8–11.99
d =	12–15.99
e =	16–19.99
f =	20–23.99
g =	24–27.99
h =	28–31.99
i =	32–35.99
j =	36–39.99
k =	40–43.99
l =	44–47.99
m =	48–51.99
n =	52–55.99
o =	56–59.99
p =	60–63.99
q =	64–67.99
r =	68–71.99
s =	72–75.99
t =	76–79.99
u =	80–83.99
v =	84–87.99
w =	88–91.99
x =	92–95.99
y =	96–100

tistate characters that also showed intraspecific polymorphism (characters 75, 84, and 85) because the raw frequency data were not obtained for these characters. For these three characters, the polymorphic OTUs were assigned more than one character state and PAUP's "interpret multiple states as uncertainty" option was invoked. Two additional multistate characters were included (characters 28 and 68), but in these cases each terminal taxon was fixed for a particular character state. The frequency coding approach is unnecessary with respect to these characters (or fixed binary characters) because frequency coding only behaves differently from standard binary coding when at least one OTU exhibits more than one character state. For example, if taxa A, B, and C are fixed for the ancestral state and taxa D, E, and F are fixed for the derived state, then under frequency coding A, B, and C will be assigned state "a" (0–3.99%) and D, E, and F will be assigned state "y" (96–100%). The ordered transformation from "a" to "y" takes one step, the same number of steps that would be assigned to this transformation using standard binary coding. As a result, a clade composed of taxa D, E, and F would be recovered and it would be supported by a single complete character state transformation (= one step). All six multistate characters were treated as unordered because no *a priori* information was available that would suggest a particular sequence through which these character states most likely evolved.

Allozyme Data Set

An allozyme data set taken from Montanucci et al. (1975) was incorporated into this analysis. These data were analyzed using a modified version of the Mabee and Humphries (1993) coding approach. Step matrices were again used, but frequency information was incorporated using Manhattan distances (Wiens, 1995). This approach allowed polymorphic allozyme data to be analyzed in a manner analogous to the frequency coding approach used for the morphology data. Alternatives to the Manhattan distance frequency approach employed in the analyses of the allozyme data include the use of polymorphic coding (terminology taken from Wiens, 1995), wherein the locus is the character and the allele is the character state, and the step matrix approach recommended by Mabee and Humphries (1993). Wiens (1995) found that the Manhattan distance frequency approach performed better than either of these alternatives (plus a number of additional alternative approaches as well). Nevertheless, combined analyses were also undertaken in which the allozyme data were analyzed using polymorphic coding and the Mabee and Humphries (1993) approaches. The allozyme data were analyzed separately in order to test for phylogenetic signal (using the bootstrap and skewness statistic). These data were then analyzed together with the morphological data generated in this study in order to determine whether together they could provide additional resolution or modify the topology produced by the morphological data alone. In the combined analyses, the multistate morphological characters were assigned a weight of 100 in order that they be weighted equally with the allozyme characters (because the Manhattan distance approach effectively weights characters 100 times more strongly than standard binary characters). For the same reason, the frequency bin characters were assigned weights of four because the frequency bin approach effectively weights characters by 24. Therefore, all of the characters were given approximately equal weight.

Ingroup Monophyly

The monophyly of crotaphytid lizards has never been questioned and, as Etheridge and de Queiroz (1988) pointed out, the most persistent taxonomic debate concerning crotaphytids has been whether or not *Gambelia* should be synonymized with *Crotaphytus* (Smith, 1946; Robison and Tanner, 1962; Weiner and Smith, 1965; Montanucci, 1969, 1978; Montanucci et al., 1975; Tanner and Banta, 1977). Nevertheless, very little character evidence has been presented supporting the monophyly of Crotaphytidae. Etheridge and de Queiroz (1988) recognized crotaphytids as a monophyletic group on the basis of a unique combination of derived, yet highly homoplastic features: the presence of posterior coracoid fenestrae and female gravid coloration, and the absence of postfrontal bones and a middorsal scale row. Frost and Etheridge (1989) considered crotaphytids to be monophyletic on the basis of three reversals: presence of palatine teeth, posterior coracoid fenestrae, and ribs on the third cervical vertebra (the last of which is only infrequently observed in crotaphytids). In each of these analyses, character support for Crotaphytidae was dependent upon its placement within the ingroup topology. The following is a list of synapomorphies of Crotaphytidae recognized in this study: presence of black oral pigmentation (reversed within *Crotaphytus*), presence of a posterolaterally projecting jugal–ectopterygoid tubercle immediately posterior to the maxillary tooth row, presence of posterior coracoid fenestrae, the tympanic crest of the retroarticular process of the mandible curves posterodorsally, the parietal and frontal strongly overlap the medial process of the postorbital, the supratemporal lies in a groove along the ventral or ventrolateral border of the supratemporal process of the parietal (reversed in most *G. silus* or convergent in *Crotaphytus* and other *Gambelia*), presence of palatine teeth, and contact of the prefrontal and jugal in the anterolateral border of the orbit.

CHOICE OF TERMINAL TAXA

The terminal taxa utilized in this study include the currently recognized species of *Crotaphytus* (*C. antiquus, C. bicinctores, C. collaris, C. dickersonae, C. grismeri, C. insularis, C. reticulatus,* and *C. vestigium*) and *Gambelia* (*G. corona*†, *G. silus,* and *G. wislizenii*). Over the course of this study, it was determined that at least one and probably two additional species should be recognized. These include two taxa currently recognized as subspecies, *C. c. nebrius* and *G. w. copei* (see taxonomic accounts for data supporting the elevation of these taxa to full species). These species were also included in the analysis.

Another population of *Gambelia* that may eventually prove to be a full species is the population of *G. wislizenii* on Isla Tiburon in the Gulf of California. The four osteological specimens examined in this study lacked autotomic fracture planes in the caudal vertebrae. Fracture planes are present in all other *G. wislizenii* (n = 19) and *G. silus* (n = 5) specimens examined, although they appeared to be fused in three of ten *G. copei*. Unfortunately, no osteological specimens were available from adjacent Sonora and it could not be determined if the absence of fracture planes is confined to this insular population. If this population proves to be a separate species, it may be the only endemic reptile or amphibian on Isla Tiburon, a land-bridge island that supports an extensive herpetofauna.

The remaining subspecies of *Crotaphytus collaris* and *Gambelia wislizenii* were not treated as separate terminal taxa because no evidence has been presented, nor has any been discovered over the course of this investigation, suggesting that these forms are discrete evolutionary entities. Rather, they are pattern or convenience classes (Frost et al., 1992), color morphs largely consistent over an extensive area, but grading smoothly into other color morphs at their boundaries.

OUTGROUP TAXA

Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) provided evidence for the monophyly of nine suprageneric groups (elevated to families in the latter study) within Iguania. Interfamilial resolution was elusive and their strict consensus tree (at the familial level) was an unresolved polytomy. However, they were able to substantially reduce the number of equally parsimonious interfamilial topologies as depicted in their 12 unrooted trees with rooting points (Fig. 1). Thus, despite the continuing lack of unambiguous interfamilial resolution, the outgroup situation has improved considerably. In this analysis, characters were considered to be polarized only when the polarity assessment was consistent with all 12 unrooted trees.

For each of the eight remaining iguanian families, exemplars were examined for the purpose of character polarization. The choice of exemplars was based whenever possible on the results of recent intrafamilial phylogenetic analyses. Thus, basal lineages have been proposed for clades within the families Phrynosomatidae (Presch, 1969; Montanucci, 1987; Etheridge and de Queiroz, 1988; de Queiroz, 1989, 1992; Wiens, 1993*a*, 1993*b*), Tropiduridae

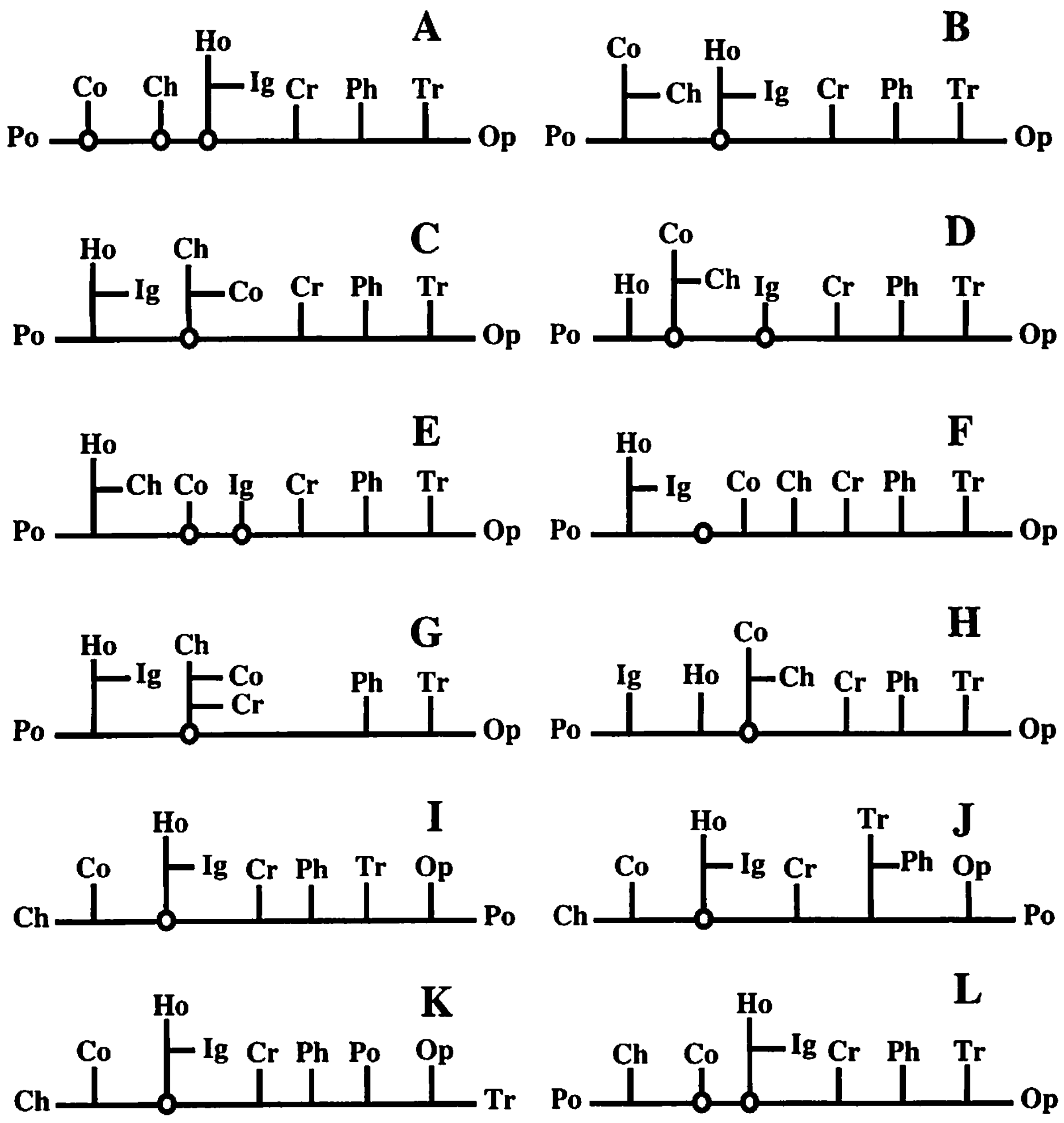

Fig. 1.—The 12 unrooted trees discovered by Frost and Etheridge (1989) in their phylogenetic analysis of iguanian lizards. The open circles represent the discovered rooting points for these unrooted trees. Ch = Chamaeleonidae, Co = Corytophanidae, Cr = Crotaphytidae, Ho = Hoplocercidae, Ig = Iguanidae, Op = Opluridae, Ph = Phrynosomatidae, Po = Polychrotidae, Tr = Tropiduridae.

(Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Frost, 1992; Pregill, 1992; Etheridge, 1995), Corytophanidae (Etheridge and de Queiroz, 1988; Lang, 1989), Hoplocercidae (Etheridge and de Queiroz, 1988), Iguanidae (de Queiroz, 1987; Norell and de Queiroz, 1991), Polychrotidae (Guyer and Savage, 1986, 1992; Etheridge and de Queiroz, 1988; Cannatella and de Queiroz, 1989), and Chamaeleonidae (Moody, 1980, 1987; Klaver, 1981; Klaver and Böhme, 1986; Hillenius, 1986, 1988; Rieppel, 1987; Frost and Etheridge, 1989). For the remaining family (Opluridae), only the phenetic analysis of Blanc et al. (1983) was available. For this lineage, I examined *Chalaradon* and as many species of *Oplurus* as possible. A list of outgroup taxa examined for this study is provided in Appendix 1 and a data matrix documenting the character states observed in these taxa is provided in Appendix 3.

MORPHOLOGY AND CHARACTER DESCRIPTIONS

Skull Roof

Premaxilla (Characters 1, 2; Fig. 2–5, 7).—The posterodorsally projecting nasal process is long and very slender in *Gambelia wislizenii* and *G. copei* (Fig. 4, 5) and broad in most *Crotaphytus* (Fig. 2, 7) and the single specimen of *G. corona*†. *Gambelia silus* (Fig. 3) occasionally has a slender but short nasal process (seven of 30) owing to its truncated snout. In *C. insularis*, the nasal process is also long and extremely narrow, which may be a consequence of elongation of the snout region. Some variation occurs in *C. vestigium* and *C. bicinctores*, both with two of 28 specimens having similarly slender nasal processes, and *C. grismeri*, with one of five having a slender nasal process, although not as extreme as that seen in *C. insularis*. Among the outgroup taxa, a narrow nasal process was observed only in *Petrosaurus mearnsi* and occasional *Uta stansburiana, Dipsosaurus dorsalis, Phymaturus palluma*, and *Ph. punae* (although the condition observed was not as extreme as that observed in *Gambelia* and *C. insularis*). Therefore, an elongate, narrow nasal process is considered to be the derived state.

In *Gambelia*, the anteromedial portion of the alveolar shelf at the articulation of the premaxilla and vomers is in the form of a strong vertical ridge. This ridge is rarely present in *Crotaphytus* (three of 51 *C. collaris*, one of four *C. antiquus*). Among the outgroup taxa, a strong vertical ridge was observed only in *Corytophanes hernandezi, Microlophus grayi*, two of three *Leiocephalus schreibersi*, and one of three *Phymaturus patagonicus zapalensis*. Therefore, a strong vertical ridge at the alveolar shelf is considered to be the derived state.

The premaxillary base is also subject to much variation in crotaphytids. In all *Gambelia*, plus many *C. antiquus, C. collaris* (primarily those formerly

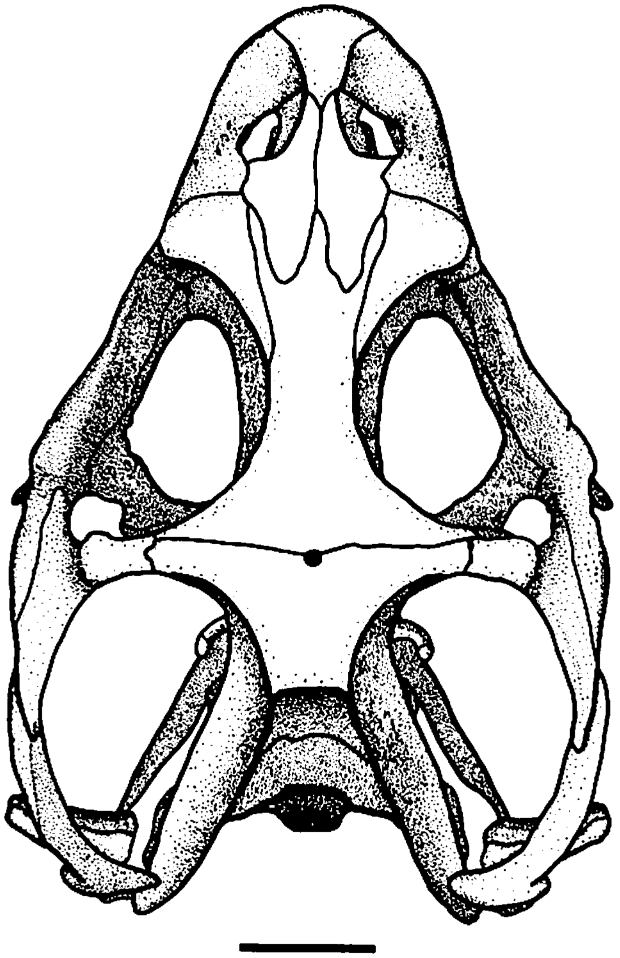

Fig. 2.—Dorsal view of the skull of *Crotaphytus dickersonae* (REE 2777, adult male, SVL = 116 mm). Scale = 5 mm.

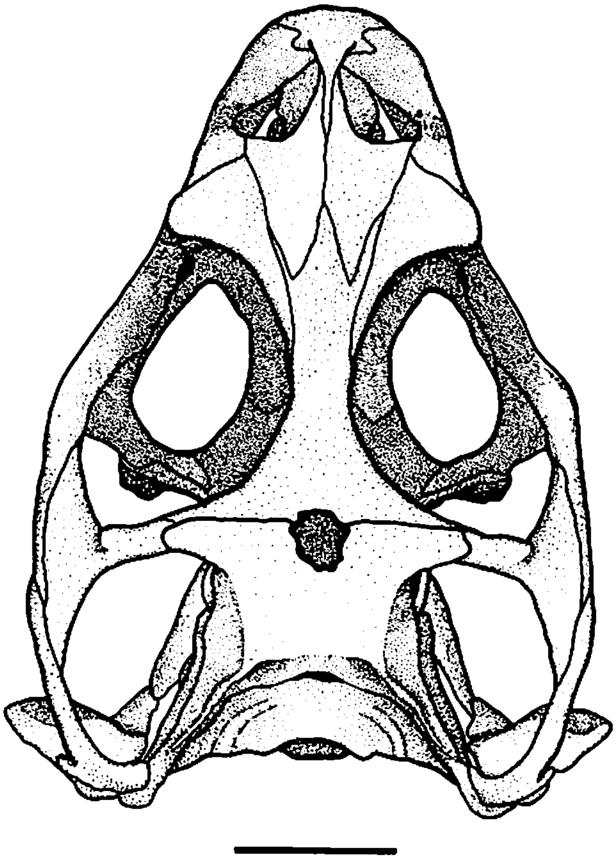

Fig. 3.—Dorsal view of the skull of *Gambelia silus* (CAS 22713, adult male, SVL = 101 mm). Scale = 10 mm.

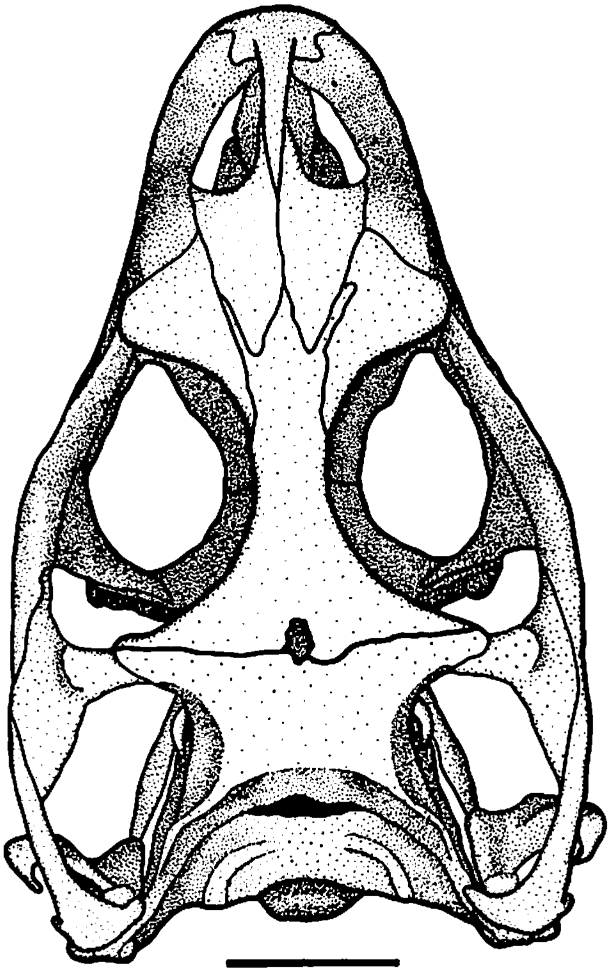

Fig. 4.—Dorsal view of the skull of *Gambelia wislizenii* (REE 2918, adult female, SVL = 119 mm). Scale = 10 mm.

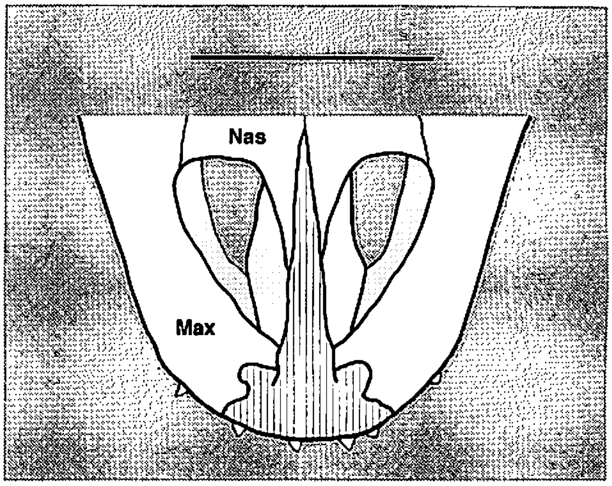

Fig. 5.—Anterior portion of the skull of *Gambelia wislizenii* (REE 2918, adult female, SVL = 119 mm) depicting the saddle-shaped premaxillary–maxillary articulations. The premaxilla is vertically hatched. Max = maxilla, Nas = nasal. Scale = 5 mm.

referred to the subspecies *C. c. auriceps* and *C. c. baileyi*), *C. grismeri, C. nebrius,* and *C. reticulatus,* the broad, laterally oriented maxillary processes give the base a rectangular shape as opposed to a trapezoidal shape (Fig. 2–4). This condition is either absent or appears rarely in *C. bicinctores, C. dickersonae, C. insularis,* and *C. vestigium.* Despite this trend, most *Crotaphytus* species display continuous variation in this feature with all intermediates between the rectangular and nonrectangular conditions present. Therefore, this character was not included in the phylogenetic study.

Nasals (Character 3; Fig. 2–4, 7).—In *Crotaphytus dickersonae* (Fig. 2), two of four *C. antiquus,* and one of 28 *C. bicinctores,* forward expansion of the nasals results in their overlap of the nasal process of the premaxilla well anterior to the posterior border of the external nares (fenestrae exonarina of Oelrich, 1956). This feature varies ontogenetically in *C. dickersonae,* with individuals of less than 81 mm snout–vent length (SVL) having incomplete contact of the nasals anteriorly (character scored only from adults). The nasals occasionally overlap the nasal process of the premaxilla anterior to the posterior extent of the external nares in *Gambelia wislizenii* and *G. copei.* However, this appears to be the result of posterior expansion of the nares rather than an anterior expansion of the nasals and is here considered to be nonhomologous. The nasals only rarely overlap the nasal process of the premaxilla anterior to the posterior extent of the external nares in the outgroup taxa. This condition was observed in *Brookesia stumpffi* and in a number of tropidurid taxa (*Ctenoblepharys adspersus,* some *Phymaturus patagonicus patagonicus, P. p. payuniae,* and *P. p. somuncurensis* [but not other *Phymaturus*], many *Leiocephalus* species, and *Microlophus grayi*). Pregill (1992) considered this feature to be absent from most basal extant *Leiocephalus,* including *L. herminieri, L. greenwayi, L. punctatus, L. inaguae, L. psammodromus,* and some *L. carinatus.* Therefore, the conditions observed in Liolaeminae, Leiocephalinae, and at least one member of Tropidurinae may be convergent. Nevertheless, nasals that overlap the nasal process of the premaxilla may be ancestral for Liolaeminae and Leiocephalinae, and,

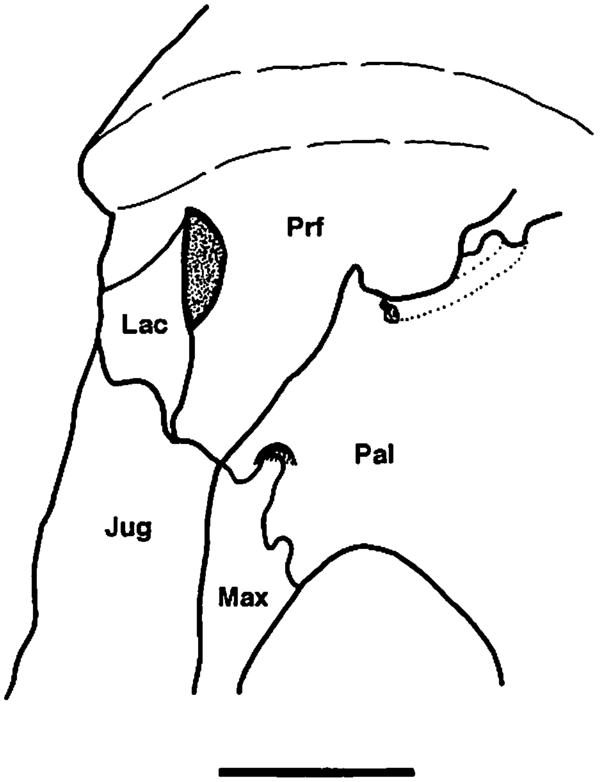

Fig. 6.—Anterior portion of the orbit showing contact of the prefrontal and jugal bones (*Crotaphytus dickersonae*, adult male, REE 2777, SVL = 116 mm). Jug = jugal, Lac = lacrimal, Max = maxilla, Pal = palatine, Prf = prefrontal. Scale = 2 mm.

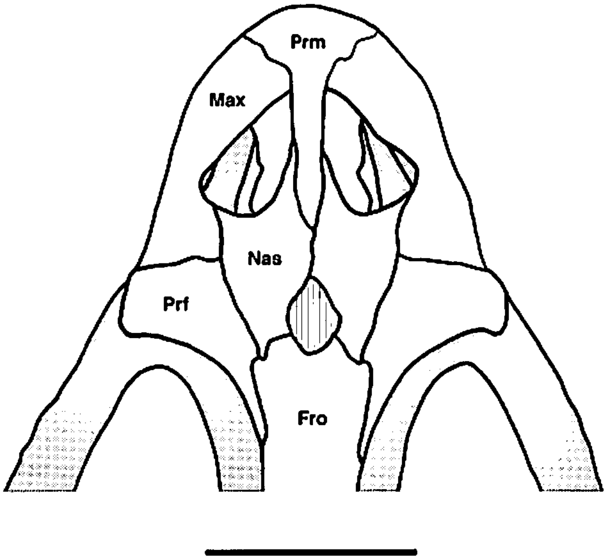

Fig. 7.—Dorsal view of the anterior portion of the skull of *Crotaphytus grismeri* (MZFC 6651, adult male, SVL = 92 mm). The vertical hatching denotes the extra frontonasal bone present in two of five specimens examined. Fro = frontal, Max = maxilla, Nas = nasal, Prf = prefrontal, Prm = premaxilla. Scale = 5 mm.

therefore, for the entire Tropiduridae. Because *B. stumpffi* and *U. acanthinurus* are the only nontropidurid iguanian taxa examined here in which the nasals overlap the nasal process of the premaxilla, it is most parsimonious to code extensive overlap of the nasal process by the nasals as the derived state.

Prefrontals (Character 4; Fig. 2–4, 6, 7).—In all crotaphytids, the palatine process of the prefrontal broadly contacts the jugal just posterior to the lacrimal foramen (de Queiroz, 1987; Fig. 6). This condition was observed in *Phrynosoma asio*, *Uma exsul*, *U. inornata*, *U. notata*, *U. scoparia*, some *Phymaturus patagonicus payuniae*, one of three *Leiocephalus macropus*, *Microlophus grayi*, one of three *Uranoscodon superciliosus*, some *Pristidactylus torquatus*, *Polychrus acutirostris*, and some *Po. marmoratus*. In *Phrynosoma asio* and *Uma* (as well as other sand lizards), this contact appears to be associated with loss of the lacrimal bone, which usually separates the prefrontal from the jugal in other iguanians. The contact of the prefrontal and jugal is considered to be the derived state and, thus, represents a synapomorphy for Crotaphytidae.

Although Norell (1989) stated that crotaphytids can be diagnosed by the derived loss of the prefrontals, clearly (as he stated elsewhere in the paper), he was referring to the loss of the postfrontals.

Frontal (Character 5; Fig. 2–4, 7, 8).—A separate, median frontonasal bone (Fig. 7) is present in two of five *Crotaphytus grismeri* (MZFC 6650, 6651). Although the sample size is small for this taxon, its presence in two specimens suggests that it is a polymorphism rather than an aberration. A similar bone was observed only in one *Phymaturus palluma* (REE 2313). Although this feature sheds no light on the phylogenetic relationships within *Crotaphytus*, it appears to represent an additional autapomorphy for the species.

The skulls of *Gambelia wislizenii*, *G. copei*, and *G. corona*† are more depressed than those of *Crotaphytus* and *G. silus*. Although this variation appears to be associated with several bones, it is perhaps best illustrated by comparing the shape and orientation of the frontal bone. In *Crotaphytus* and *G. silus*, this bone is more strongly convex, while in

G. wislizenii, G. copei, and *G. corona*†, this bone usually is relatively flat, providing little height to the midorbital region of the skull. A description of the frontal bone only partially explains the complex variation in skull height within crotaphytids. Therefore, the character is here defined as "skull depressed" or "skull vaulted." Although a vaulted midorbital region of the skull is the more common condition within Iguania, this character could not be polarized.

Norell (1989) described the fossil taxon *Gambelia corona*† based in part on a broad frontal that is transversely concave with supraorbital ridges. Many *Gambelia* have broad frontals; however, the dorsal surface is usually flat. Only one of 53 *G. wislizenii* (REE 2792) had weakly developed supraorbital ridges with a slight concavity and no *G. copei* were examined with this condition. *Gambelia silus* also usually lack the supraorbital ridges; however, three of 31 had well-developed supraorbital ridges with strong transverse concavity. Although this condition cannot be considered unique to *G. corona*†, it appears to be a useful diagnostic feature for the species. Additional fossil material will be required in order to determine if this character is variable as in other *Gambelia.* The frontal may bear supraorbital ridges that give it a concave appearance in some *Crotaphytus,* although, as in *Gambelia,* it is only infrequently present. Among the outgroup taxa, a transversely concave frontal was observed in *Enyalioides laticeps, Basiliscus basiliscus, B. plumifrons, B. vittatus, Corytophanes hernandezi,* some *Corytophanes cristatus,* some *Laemanctus longipes,* some *Phymaturus palluma,* some *Leiocephalus carinatus, Uranoscodon superciliosus, Uromastyx hardwickii, Physignathus lesueurii, Hydrosaurus amboiensis, Brookesia kersteni, Enyalius perditus, Polychrus marmoratus,* and *P. acutirostris.* Therefore, this character could not be polarized.

Norell (1989) considered the frontoparietal suture anterior to the posterior extent of the orbit to be an additional autapomorphy of *Gambelia corona*†. Although it is possible that this condition is an artifact resulting from damage to the fossil (dorsoventral compression), it does appear as though the frontoparietal suture was indeed anterior to the posterior extent of the orbits. The postorbitals project more posteriorly in *G. corona*† than in other crotaphytids, which may play some role in the anterior placement of the suture. Although this character is not phylogenetically informative, it provides a diagnostic autapomorphy for the species.

In articulated skulls of some iguanians, the suture that binds the frontal with the nasals and prefrontals takes the form of a "W." However, this shape results from the extensive overlap of the frontal by the nasals and prefrontals. The underlying anterior border of the frontal is often squared off or may possess two small lateral processes that project anteriorly. In all crotaphytids, the anterior border of the frontal bears three well-developed processes, two lateral projections and one medial projection, that extend forward equidistantly. This condition occurs sporadically within Iguania and could not be polarized. Therefore, this feature was not considered in the phylogenetic analysis.

Postfrontals.—The postfrontals are small bones that form part of the posterior border of the orbits in many iguanian species, but are absent or fused in all crotaphytids. Postfrontals are absent or occasionally present as minute elements in *Phrynosoma* and the phrynosomatid sand lizards, some *Phymaturus* (*Phymaturus palluma,* some *Phymaturus punae*), oplurids, *Polychrus* (contra Frost and Etheridge, 1989; verified in *P. acutirostris* and *P. marmoratus*), *Basiliscus, Corytophanes,* and Chamaeleonidae. Although the absence or fusion of the postfrontal bones may eventually prove to be a synapomorphy for Crotaphytidae, the currently unresolved nature of iguanian phylogeny prevents polarization of this character.

Postorbitals (Characters 6, 7; Fig. 2–4, 8).—The dorsal process of the postorbital is roughly triangular in cross section in all crotaphytids. The dorsomedial aspect is completely overlapped by the frontal and parietal while the ventral portion is exposed. Thus, in an articulated skull it appears as though a long process projects medially beneath the overlying frontal and parietal. This condition appears to be more extreme in *Crotaphytus* because the parietal and frontal overlap the postorbital more laterally in these lizards. However, the condition of the postorbital does not vary significantly between *Crotaphytus* and *Gambelia.* In the outgroup taxa, the frontal and parietal usually meet the dorsomedial portion of the postorbital without overlapping it extensively; the only obvious exceptions are hoplocercids, corytophanids, one of two *Uromastyx acanthinurus,* basal agamines (*Physignathus* and *Hydrosaurus amboiensis*), and *Enyalius iheringi.* A strong degree of overlap at this joint, which appears to provide additional structural support, is tentatively recognized as a synapomorphy of Crotaphytidae.

The angle of the dorsal process often differs between *Crotaphytus* and *Gambelia.* In *Crotaphytus,* the process is transversely oriented, while in *Gambelia* it is often anteromedially oriented. In many cases this difference is very obvious. However, continuous variation within *Gambelia* prevented the inclusion of this character in the phylogenetic analysis.

The postorbital meets the jugal and squamosal in a tongue-in-groove articulation. In crotaphytids, the postorbital bears the shallow groove in which the jugal and squamosal lie. This condition is more developed in *Gambelia,* which bears a large flare that broadly overlaps the jugal and squamosal on the medial side of the joint. This feature is difficult to evaluate in the outgroups due to the paucity of disarticulated skulls. However, it appears that this condition is widespread within Iguania and it was not included in the phylogenetic analysis.

Finally, in *Gambelia copei* (eight of eight), relatively few *G. wislizenii* (four of 49; REE 425, 2792; UIMNH 43378–79), and four of 31 *G. silus* (KU 121753, 121761, 121766, 121768), there is a small projection or tubercle on the anterolateral surface of the postorbital at the posterior edge of the orbit (= character 7). In *G. copei,* it is usually larger and more robust than in other *Gambelia.* This small tubercle may function as an additional attachment point for the skin of the head as does the larger dorsal tubercle. The presence of this tubercle appears to be unique within Iguania and may be a synapomorphy for *Gambelia,* although its more developed state may be further derived in *G. copei.* Nevertheless, this feature is coded as a binary character with the absence of a tubercle coded as the ancestral condition (state 0) and the presence of a tubercle as the derived condition (state 1). Because they were polymorphic with respect to this character, *G. wislizenii* and *G. silus* were assigned states c and d respectively.

Parietal (Characters 8, 9; Fig. 2–4, 8).—The parietal is a median bone that represents the major element of the skull roof. Its complex shape includes a trapezoidal roof with short anterolateral processes and long posterolaterally projecting, laterally compressed supratemporal processes. This shape changes ontogenetically, although not to the extent seen in some iguanids, polychrotids, and *Leiocephalus* (Etheridge, 1959; de Queiroz, 1987; Pregill, 1992). In juveniles, the parietal roof is roughly square, the crests of the supratemporal processes are less robust and project nearly directly posteriorly. During ontogeny, the posterior edge of the parietal roof becomes increasingly constricted such that the lateral borders of the roof converge. This gives the roof a trapezoidal shape with the supratemporal processes projecting posterolaterally rather than posteriorly. Late in ontogeny, ridges may form along the lateral and posterior borders of the parietal roof giving the central portion a depressed appearance. The degree of constriction of the posterior border of the parietal roof during ontogeny differs between *Crotaphytus* (Fig. 2) and *Gambelia* (Fig. 3, 4). In *Gambelia,* the roof remains relatively broad posteriorly throughout ontogeny and remains approximately twice the width of the narrowest portion of the frontal bone. In *Crotaphytus* (particularly males) the posterior border of the parietal shelf becomes more constricted such that it is approximately equal in width to the frontal bone or slightly wider. This constriction is often most dramatic in adult male *C. dickersonae,* although enough overlap occurs between species of *Crotaphytus* that this was not considered as a separate character state. There is much variation in the degree of constriction of the parietal roof within Iguania, with the basal lineages of all but three families (Phrynosomatidae, not constricted; Corytophanidae, constricted; Hoplocercidae, constricted) having representatives with both states. Although the polarity of the character could not be determined, *Gambelia* and *Crotaphytus* always differ in the degree of constriction of the parietal roof. Therefore, this feature was coded as an unpolarized binary character with the *Gambelia* condition coded as state 0 and the *Crotaphytus* condition coded as state 1.

The supratemporal processes are extremely robust in *Crotaphytus* and, in lateral view, project well above the temporal arches (Fig. 8). The lateral faces of the processes are also concave. The robust character of the processes gives broad surface area for the origin of the hypertrophied jaw adductor muscles that these lizards possess. In all *Crotaphytus* examined except some eastern *C. collaris* (13 of 51 specimens), the supratemporal processes are strongly inflected ventrad at their distal ends. The skulls of some eastern *C. collaris* tend to be more dorsoventrally compressed, which may result in less inflected supratemporal processes. *Gambelia* also possess ventrally oriented processes, although of a different character. The crests of the supratemporal processes are well developed anteriorly, but quickly taper posteriorly, usually terminating anterior to the articulation of the process with the squamosal. By contrast, in *Crotaphytus,* the crests of the supratemporal processes continue posteriorly well beyond the squamosal to its terminus. As a result, in *Gambelia,*

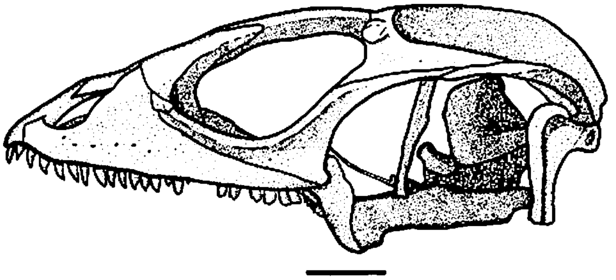

Fig. 8.—Lateral view of the skull of *Crotaphytus dickersonae* (REE 2777, adult male, SVL = 116 mm). Scale = 5 mm.

the processes appear less robust and do not arch as far above the plane of the parietal roof. This variation, which can be used to quickly differentiate between skulls of these genera, could not be polarized due to variation in the outgroups.

Supratemporals (Character 10; Fig. 9, 10).—The supratemporals are small paired bones that lie in ventrolateral grooves in the supratemporal processes of the parietal in most crotaphytids (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). The supratemporals are more exposed posterolaterally and form the major portion of the process at its articulation with the quadrate and squamosal. The tongue-in-groove articulation of each supratemporal with the parietal is well developed in all crotaphytids except *Gambelia silus* (Fig. 9, 10). Indeed, in most *G. silus* that could be coded for this character (25 of 28), the supratemporal does not sit in a groove, but lies along the lateral surface of the supratemporal process (Fig. 10). This variation is occasionally observed in *G. wislizenii* (four of 49), *C. antiquus* (one of four), and *C. collaris* (one of 51). In iguanian lizards, the tongue-in-groove relationship between the supratemporal and supratemporal process is seen only in crotaphytids and the tropidurid genus *Liolaemus* and therefore is here considered to be derived within Crotaphytidae. The condition observed in *G. silus* may be a reversal because some individuals do possess the rare grooved condition seen in few iguanian lizards.

Septomaxillae (Character 11; Fig. 2–5, 7).—The septomaxillae are paired sheets of bone situated in the anteromedial nasal capsule where they form the floor of the nasal passages and the roof over the Jacobson's organ (Oelrich, 1956; Jollie, 1960). In *Gambelia wislizenii* and *G. copei*, the septomaxillae are slender and more elongate than in either *G. silus* or *Crotaphytus*. It is likely that this condition is

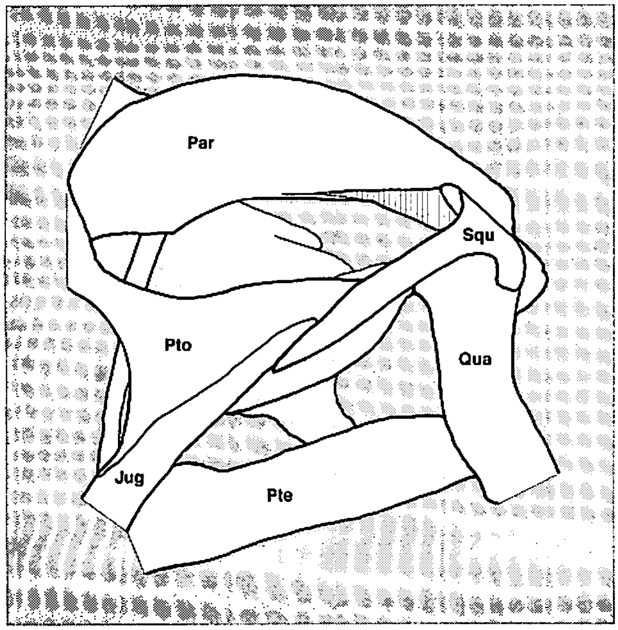

Fig. 9.—Supratemporal region of *Crotaphytus vestigium* (REE 2935, adult male, SVL = 125 mm). The vertical hatching denotes the exposed portion of the supratemporal bone. Jug = jugal, Par = parietal, Pte = pterygoid, Pto = postorbital, Qua = quadrate, Squ = squamosal. Scale = 5 mm.

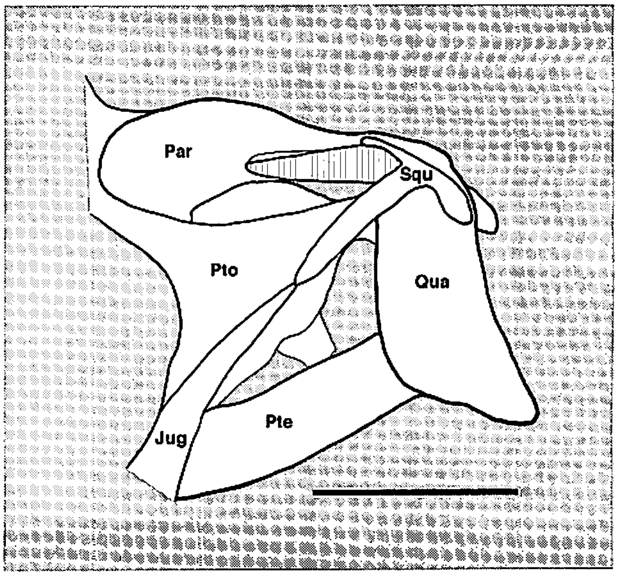

Fig. 10.—Supratemporal region of *Gambelia silus* (CAS 22713, adult male, SVL = 101 mm). The vertical hatching denotes the exposed portion of the supratemporal bone. Jug = jugal, Par = parietal, Pte = pterygoid, Pto = postorbital, Qua = quadrate, Squ = squamosal. Scale = 5 mm.

associated with the more elongate snout seen in this species. This hypothesis is corroborated by the relatively slender septomaxillae seen in *C. bicinctores, C. dickersonae, C. grismeri, C. insularis,* and *C. vestigium,* which also have relatively elongate snouts. However, these taxa do not have the extreme condition present in *G. wislizenii* and *G. copei.* Elongate, slender septomaxillae are rarely observed within Iguania. In *Oplurus* (*O. cuvieri* and *O. quadrimaculatus*), they are extremely slender, almost splinter-like, while in certain other iguanians (*Phrynosoma asio, P. orbiculare, P. coronatum,* some *Dipsosaurus dorsalis*) they are slender, although to a lesser degree. Elongate, slender septomaxillae are considered to be the derived state. However, septomaxillae are often destroyed during the preparation of skeletons and many outgroup taxa are not represented here. Because this feature appears to be associated with the much more elongate snout that occurs in *G. wislizenii* and *G. copei,* this character is treated as a character complex (although all of the differences that appear to be associated with an elongate snout cannot be polarized as can the septomaxillae conditions).

Maxillae (Characters 12, 13; Fig. 2–5, 7, 8).—The premaxillary process contacts the premaxilla anteriorly by means of an overlapping sheet of bone. It includes a well-developed shelf that passes posterior to the nasal process of the premaxilla and acts as the anterior wall of the external naris. The septomaxilla contacts the posterodorsal edge of this shelf while posteroventrally the shelf is contacted by the vomer. In *Gambelia wislizenii, G. silus,* and five of eight *G. copei* (absent in REE 2798, 2802, 2805), a protrusion of the premaxillary process overlaps the lateral edge of the premaxilla such that the suture is saddle-shaped (Fig. 3–5). This condition is only rarely observed in the outgroups (present in some *Chalaradon madagascariensis, Petrosaurus mearnsi, Urostrophus vautieri,* some *Pristidactylus torquatus, Enyalius brasiliensis, E. pictus, Phymaturus punae,* some *P. palluma, Leiocephalus melanochlorus,* and some *L. carinatus*) and is considered to be the derived state.

The dorsally directed nasal process of the maxilla contacts the nasal, prefrontal, and lacrimal bones and forms the posterolateral wall of the external naris and the lateral wall of the nasal capsule. A canthal ridge is present on the nasal process and extends from the rugose protuberance of the prefrontal to the base of the premaxillary process near the posterolateral corner of the external naris. The angle of the canthal ridge, as well as the posterior margin of the external naris, is much greater (greater than 45 degrees) in *Crotaphytus, Gambelia corona*†, and *G. silus* than it is in *G. wislizenii* and *G. copei* due to the elongate snout of the latter two species. Several potentially useful characters are associated with the longer snout of *G. wislizenii* and *G. copei,* including the more elongate septomaxillae and vomers. However, as each of these appears to be linked to rostral elongation, they are considered as one character (see septomaxillae) in this analysis.

Ventromedially, a thickening of the maxilla forms a shelf-like process that overlaps the palatine. This shelf projects further medially in *Crotaphytus* (Fig. 11, 12) than in *Gambelia* and is more nearly triangular. In *Gambelia,* the shape of the process is in the form of a low, rounded arch. There is extensive variation in the outgroups with regard to this feature and it was left unpolarized.

Jugals (Characters 14, 15; Fig. 2–4, 8, 11).—The general shape of the jugal varies little in crotaphytids although three potentially useful variations were observed. A ridge, or thickening, is found on the external surface of the jugal, extending from its immediate anterior end posteriorly just beyond the jugal's articulation with the postorbital. The ridge is thicker in *Crotaphytus* than in *Gambelia* and is most developed in *C. reticulatus.* The function of this ridge is uncertain, although it provides the surface for attachment of the subocular scales. A lateral ridge is present on the jugal in many iguanians, although it is usually less strongly developed than that of *Crotaphytus.* Although this may eventually prove to be a phylogenetically useful character, it was not considered in this analysis.

All crotaphytids possess an enlarged tubercle posterior to the termination of the maxillary tooth row (Fig. 2, 8, 11). This tubercle is actually comprised of both the jugal, which forms the anterior portion, and the ectopterygoid, which forms the posterior portion. The function of the tubercle appears to be as an attachment site for the ligamentum quadratomandibulare. The size of the tubercle is interspecifically variable, with *Crotaphytus antiquus, C. collaris, C. dickersonae, C. nebrius,* and *C. reticulatus* having very large tubercles and the remaining taxa having small ones. Despite this variation in size, the presence or absence of a tubercle was coded as a binary character. In the outgroups, a similar tubercle is present in the leiosaurs *Pristidactylus, Diplolaemus,* and *Leiosaurus* and a less similar laterally compressed tubercle is present in some chamaeleonids

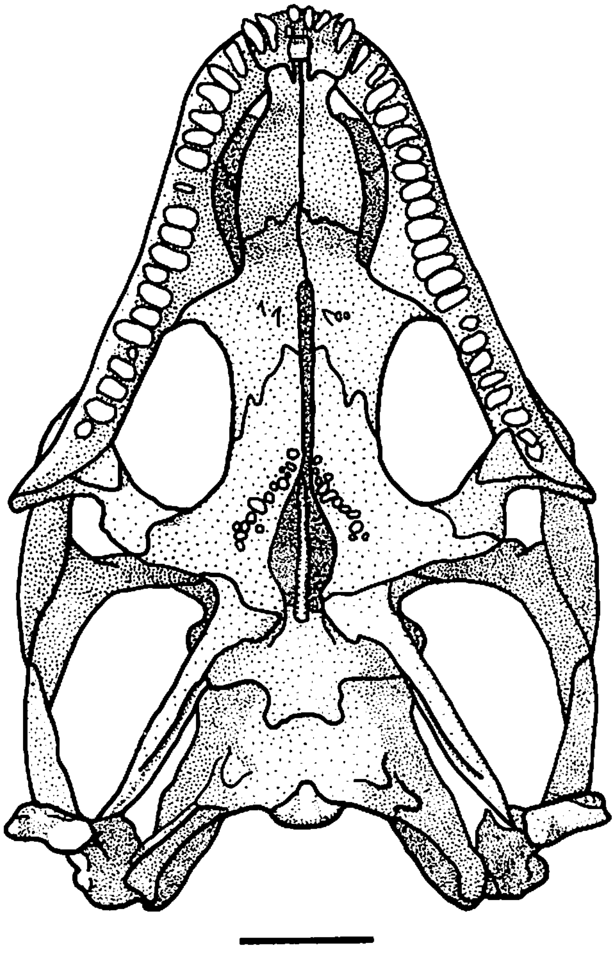

Fig. 11.—Ventral view of the skull of *Crotaphytus dickersonae* (REE 2777, adult male, SVL = 116 mm). Scale = 5 mm.

(*Leiolepis belliana, Physignathus lesueurii*). Therefore, the presence of a tubercle is considered to be the derived state and represents a synapomorphy for Crotaphytidae.

There is also variation in the angle of the jugal where it serves as the ventrolateral border of the orbit. In *Crotaphytus*, the medial face of the jugal is oriented dorsolaterally at about a 45-degree angle over most of its length. In *G. wislizenii, G. copei*, and 15 of 31 *G. silus*, the medial face becomes progressively more vertical anteriorly until it articulates with the palatine, lacrimal, and prefrontal. As a result, the region of articulation of the three bones in *Gambelia wislizenii, G. copei*, and some *G. silus* is box-like because the jugal meets the palatine and prefrontal at perpendicular angles. In *Crotaphytus* and some *G. silus*, the jugal meets the prefrontal in a smooth, rounded arc. The box-like condition of the ventrolateral border of the orbit was approached only in *Petrosaurus mearnsi, Uta stansburiana, Uma* (but not *Callisaurus, Cophosaurus*, or *Holbrookia maculata*), one of two *Enyalioides laticeps*, and *Leiolepis belliana* and is therefore considered to be the derived state within Crotaphytidae.

PALATE

Vomers (Character 16; Fig. 11, 12).—In *Crotaphytus insularis* and *C. vestigium*, a separate pair of small bones, here termed extravomerine bones, may be present posteromedially where the vomers and palatines meet (Fig. 12). These medially contacting bones appear to be the result of secondary ossification centers in the vomers. In many specimens, this additional bone is present on one side only and the region where the bone is absent is filled in by the vomer from that side. Extravomerine bones are present in all five *C. insularis* available for study, although it is found on the right side only in one specimen (REE 2797). It is also found on at least one side in ten of 27 *C. vestigium*. Extravomerine bones are not present in the outgroup taxa examined here and no evidence has been discovered documenting their presence in other lizard species. Therefore, the presence of either one or two extravomerine bones is considered to be the derived state.

Palatines (Character 17; Fig. 6, 11, 12).—In *Crotaphytus*, the dorsal surface of the maxillary process usually bears the palatine foramen (Fig. 6), which may be situated in the suture of the maxillary process and the prefrontal or completely within the palatine. In one *C. collaris* (USNM 220216), the foramina were located entirely within the palatine processes of the prefrontals. A well-developed, transversely oriented canal, associated with the intermediate palatine branch of nerve VII (Oelrich, 1956), projects medially from the palatine foramen (Fig. 6). In *Gambelia*, a palatine foramen is only rarely evident (five of 43 *G. wislizenii*, zero of eight *G. copei*, two of 30 *G. silus*), although the canal, and presumably the intermediate palatine branch of nerve VII, are present. Instead of passing through the prefrontal and palatine bones, the tube passes through the connective tissue medial to the palatine process of the prefrontal along the lateral border of the orbitonasal fenestra. The absence of a palatine foramen in the great majority of *Gambelia* appears to be the result of the narrower palatine process of the prefrontal found in this taxon, rather than the absence or rerouting of the intermediate palatine branch of nerve VII. Some variation was observed within *Crotaphytus* including *C. collaris* (foramen present in seven of 51), *C. grismeri* (three of five), and *C. reticulatus* (22 of 26). The outgroup taxa are also extremely variable with respect to this feature, preventing its polarization. Phylogenetically useful variation was also observed in the palatine foramina of *Phymaturus*. In all specimens of *Phymaturus* examined, the foramina were much larger proportionally than those of any other iguanian taxon examined.

Pterygoids (Characters 18–20; Fig. 2–4, 8, 11).—The transverse process of the pterygoid of *Crotaphytus* bears a sharp vertical crest near its lateral end. This crest is very weak or absent in *Gambelia*. A strong vertical crest is present in many iguanian species and its absence may be a synapomorphy for *Gambelia*. However, this crest appears to be associated with a more easily definable character of the ectopterygoid and its description is given in the discussion of that element.

The transverse processes of *Crotaphytus reticulatus* and *C. dickersonae* are more ventrally expanded in comparison to the other crotaphytids. This condition is especially extreme in adult male *C. dickersonae*, which bear a well-developed crest that extends along the ventral edge of the entire transverse process terminating at, or near, the interpterygoid vacuity. This crest descends ventrally to a degree seen in no other crotaphytid species. Although it is difficult to compare this feature across a broad range of taxa with very different pterygoid morphologies, a strongly developed crest appears to be present in many corytophanids, chamaeleonids, and polychrotids, as well as within large iguanids. Therefore, this character was left unpolarized.

In *Gambelia*, the quadrate processes are approximately one-third shorter as a percentage of skull length than they are in *Crotaphytus*. In *Crotaphytus*, the posterior part of the skull is clearly longer than that of *Gambelia* and this is best illustrated by comparing the posterior extents of the quadrate processes of the pterygoids, the supratemporal processes, and the paraoccipital processes with the posterior extent of the occipital condyle. In adult *Crotaphytus*, all three processes project well posterior to the occipital condyle (Weiner and Smith, 1965; Fig. 2, 11), while in *Gambelia*, they reach a point roughly equidistant with the condyle (Fig. 3, 4). This condition is subject to considerable ontogenetic variation, with juveniles of both genera having the three processes extending posteriorly to a point equidistant with the occipital condyle until they reach an SVL of approximately 80–85 mm. At this point in ontogeny, the processes begin to project further posteriorly in *Crotaphytus* than in *Gambelia*. The condition observed in adult *Crotaphytus* appears to be apomorphic and was only observed in large male *Basiliscus basiliscus*, *Pristidactylus* (as well as *Diplolaemus* and *Leiosaurus*), *Uromastyx acanthinurus*, *U. benti*, *U. microlepis*, and *Physignathus lesueurii*. This condition may represent an adaptation for more powerful jaw adduction in these lizards.

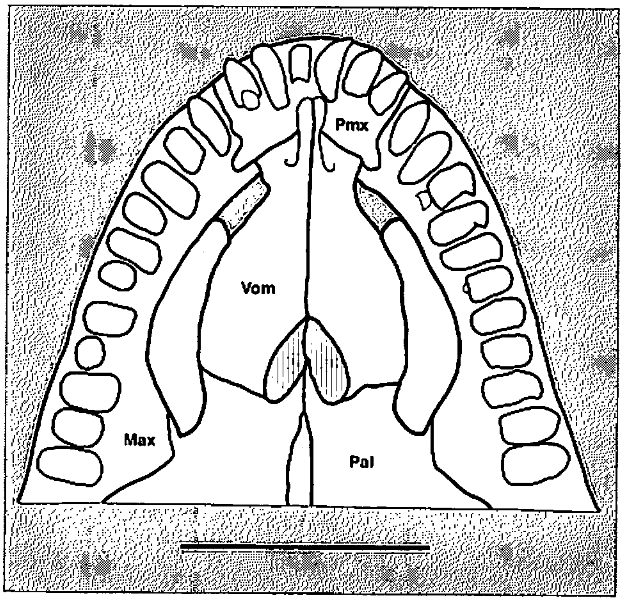

Fig. 12.—Ventral view of skull of *Crotaphytus vestigium* (REE 2826, adult male, SVL = 105 mm) showing the extravomerine bones (vertically hatched) present in *C. insularis* and many *C. vestigium*. Scale = 5 mm.

In *Crotaphytus* and *Gambelia silus*, the quadrate processes project posterolaterally at a greater angle (approximately 26–31 degrees) than in *G. wislizenii* and *G. copei* (approximately 18 degrees). Most of the outgroup taxa appear to be similar to *Crotaphytus* and *G. silus* with respect to this feature, although enough variation was observed that the character was left unpolarized.

Ectopterygoids (Character 21; Fig. 2–4, 11).—In *Crotaphytus*, the transverse process of the pterygoid bears a strong vertical crest just medial to its articulation with the ectopterygoid. In *Gambelia*, this crest is weakly defined and this appears to be associated with the morphology of the ectopterygoid. The dorsal surface of the ectopterygoid is in the form of a sharp transverse edge or ridge that extends to the termination of the medially projecting process.

This ridge bears a posterior projection in *Crotaphytus* that overlaps the strong vertical crest of the transverse process. The ridge does not bear a strong posterior projection in *Gambelia*, instead being straight or nearly so. Presence or absence of a posterior projection of this ridge are coded as separate character states. However, there is much variation in the outgroups and this character could not be polarized.

The ectopterygoid also bears a strong posterolateral process that is sutured to a similar process of the jugal. Together they form the tubercle that projects posterolaterally just beyond the termination of the maxillary tooth row (see description of jugal above).

BRAINCASE

Parabasisphenoid (Character 22; Fig. 11).—Projecting anteriorly from the basisphenoid is the long, blade-like parasphenoid process. Although this is a separate osseous element, it is fused with the basisphenoid in postembryonic crotaphytids and, following Jollie (1960:fig. 3), they are here treated as a single element, the parabasisphenoid.

The posterior suture of the parabasisphenoid with the basioccipital differs between *Gambelia* and *Crotaphytus*. In *Gambelia*, the parabasisphenoid bears long posterolateral processes that extend to the sphenoccipital tubercles. These processes are absent or extend only slightly beyond the transverse plane of the parabasisphenoid–basioccipital suture in most *Crotaphytus* examined (Fig. 11), although they may occasionally reach the base of the lateral process of the basioccipital. The posterolateral processes never were observed to reach the sphenoccipital tubercles, although they nearly reached the tubercle in two of 29 *C. collaris* (LLG 62, REE 2948).

The majority of the outgroup taxa have long posterolateral processes of the parabasisphenoid that reach or nearly reach the sphenoccipital tubercles. Exceptions occur within the families Phrynosomatidae, Chamaeleonidae, Tropiduridae, and Polychrotidae. In Phrynosomatidae, short processes are present in *Petrosaurus*, *Uta*, *Urosaurus graciosus*, and *Sator grandaevus* (but not *Sceloporus*, at least those examined here; Appendix 1), while in *Phrynosoma* and the sand lizards they are long. Therefore, short processes may be an additional synapomorphy for *Petrosaurus* plus the *Sceloporus* group, with a reversal in *Sceloporus*.

Within Chamaeleonidae, short processes are present in *Leiolepis belliana*, but not *Uromastyx* or the basal agamines *Physignathus lesueurii* and *Hydrosaurus amboiensis*. Within chamaeleonines, *Brookesia stumpffi* has short processes, while all of the remaining chamaeleonines examined (Appendix 1) except *Chamaeleo kerstenii* have long processes. In *C. kerstenii*, the basioccipital is displaced forward by the exoccipitals such that it does not form the ventral portion of the occipital condyle. As a result, the basioccipital tubercles are found on the exoccipitals rather than the basioccipital. Thus, the homology of the posterolateral processes (or lack thereof) of this species is questionable.

In tropidurids, the processes are short in *Ctenoblepharys*, *Liolaemus*, and some *Leiocephalus* (short in *L. barahonensis*, *L. carinatus*, *L. lunatus*, *L. macropus*, and *L. psammodromus;* long in *L. greenwayi*, *L. melanochlorus*, *L. personatus*, *L. schreibersi*, *L. stictigaster*, and *L. vinculum*), but long in all of the Stenocercini and Tropidurini examined (Appendix 1) except *T. spinulosus* and *T. melanopleurus*, which are nonbasal taxa (Frost, 1992).

Within polychrotids, the processes are short in *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, the anoles, the para-anoles (intraspecifically variable in *Urostrophus vautieri*), and some *Polychrus acutirostris* (but not *P. marmoratus*), but long in *Enyalius*.

Long posterolateral processes represent the ancestral condition in Hoplocercidae, Opluridae, Corytophanidae, Iguanidae, and Chamaeleonidae, and the polarity of this character is equivocal for Phrynosomatidae and Tropiduridae (but long processes may be ancestral for Tropiduridae). It is most parsimonious to assume that short posterolateral processes were present in the common ancestor of Polychrotidae. Thus, the presence of short posterolateral processes are treated as the derived state within Crotaphytidae.

Additional intergeneric variation was also observed in the parabasisphenoid. At the anterodorsal end of the basisphenoid is a depression, the sella turcica, that houses the pituitary gland. In adult *Crotaphytus*, the sella turcica usually is elevated such that in lateral view, it is visible above the quadrate process of the pterygoid. In *Gambelia*, the sella turcica is more depressed and is rarely visible above the quadrate process. However, continuous variation exists in this characteristic and it was omitted from the phylogenetic study.

MANDIBLE

Dentary (Fig. 13, 14).—In many iguanian lizards, the dentary is tubular anterior to the splenial and

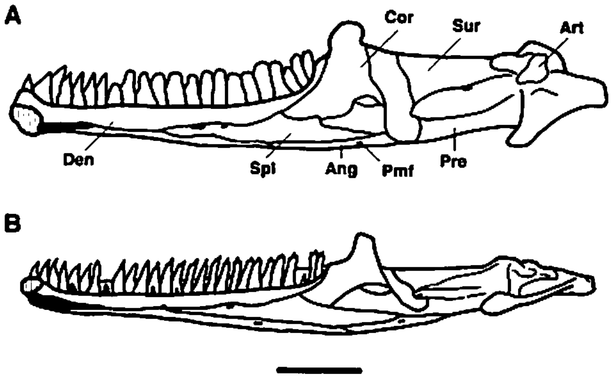

Fig. 13.—Lingual view of the right mandible of (A) *Crotaphytus reticulatus* (REE 2912, adult male, SVL = 122 mm) and (B) *Gambelia copei* (REE 2800, adult female, SVL = 123 mm). Ang = angular, Art = articular, Cor = coronoid, Den = dentary, Pmf = posterior mylohyoid foramen, Pre = prearticular, Spl = splenial, Sur = surangular. Scale = 5 mm.

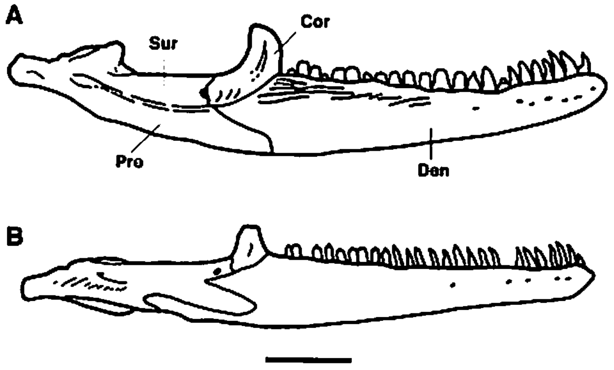

Fig. 14.—Labial view of the right mandible of (A) *Crotaphytus reticulatus* (REE 2912, adult male, SVL = 122 mm) and (B) *Gambelia copei* (REE 2800, adult female, SVL = 123 mm). Cor = coronoid, Den = dentary, Pre = prearticular, Sur = surangular. Scale = 5 mm.

completely encloses Meckel's cartilage. In crotaphytids, the tubular nature of the dentary is incomplete. The anterior end of the dentary is open, while posteriorly the groove is closed, but not fused. In *Crotaphytus*, with the exception of *C. grismeri*, the groove is usually closed over less than one-half of its length anterior to the splenial and there is relatively consistent interspecific variation in this characteristic. In *C. collaris*, *C. nebrius*, and *C. reticulatus*, Meckel's groove is often open over its entire length anterior to the splenial, and most of the remaining specimens have the groove closed over less than one-third of its length. In *C. antiquus* and *C. dickersonae*, the groove is not open over its entire length, but as in the above-mentioned taxa, it was nearly always closed over less than one-third of its length. In *C. bicinctores*, *C. insularis*, and *C. vestigium*, Meckel's groove is usually closed over between one-third and one-half of its length anterior to the splenial and was only once observed to be open over its entire length (*C. vestigium*, REE 2811). *Crotaphytus grismeri* is unique among *Crotaphytus* in that Meckel's groove is closed over between approximately 50 percent and 70 percent of its length in all specimens examined (five of five). Norell (1989) noted that in *Gambelia*, the groove is usually closed over two-thirds of its length anterior to the splenial. Unfortunately, this condition is much more variable in *Gambelia* than in *Crotaphytus*, and although the groove in most specimens is closed over greater than one-half of its length anterior to the splenial, 12 of 30 *G. silus*, two of nine *G. copei*, and 12 of 45 *G. wislizenii* had a condition similar to that observed in *Crotaphytus*, with the groove closed over less than half of its length anterior to the splenial. Because of this variation, this character was not considered in the phylogenetic analysis.

Norell (1989) also considered an elongate dentary (with a posterior process projecting posterior to the superior apex of the coronoid, Etheridge and de Queiroz, 1988) to be a synapomorphy for Crotaphytidae. Although this character state was found to be derived in their phylogenetic analysis of pleurodont iguanians (possibly a paraphyletic assemblage with respect to acrodont iguanians [Chamaeleonidae]), this state is widespread within Iguania and may be a synapomorphy for a group more inclusive than Crotaphytidae.

The dentary bears between three and eight mental foramina anteriorly. In *Crotaphytus*, the mental foramina are usually restricted to the distal end of the dentary, while in *Gambelia* they may extend posteriorly to the midpoint of the bone. Continuous variation in this feature prevented its inclusion in the phylogenetic analysis.

Angular (Characters 23, 24; Fig. 13).—In *Crotaphytus*, the exposed portion of the angular extends further anteriorly than in *Gambelia wislizenii* and *G. copei*. Defining states for this character is complicated by the variation that exists in those structures that may serve as reference points. For this reason, two points of reference are included in the description of this character. In adult *Crotaphytus*, with very few exceptions, the angular extends anteriorly at least to the fourth tooth (counting from the rear of the tooth row) and usually well beyond this point. Juveniles are not always comparable because their teeth are relatively larger than those of adults and are often widely spaced. The angular also extends well beyond the anterior extent of the coronoid in both adults and juveniles. In *G. wislizenii* and *G. copei*, the angular was never observed to reach the fourth tooth (from the rear of the tooth row) and rarely reached beyond the first. In most specimens, the angular does not extend as far anteriorly as does the coronoid. In *C. bicinctores*, *C. grismeri*, and *G. silus*, the anterior extent of the angular shows continuous variation with most specimens having an intermediate condition but others with character states similar to those observed in *G. wislizenii* and *G. copei* or the remaining species of *Crotaphytus*. Because of this continuous variation in these three taxa, I have coded each as unknown for this character. With respect to the outgroup taxa, the angular projects well anteriorly in chamaeleonids, hoplocercids, the corytophanids *Basiliscus basiliscus*, *B. vittatus*, *B. plumifrons*, some *Corytophanes cristatus*, *C. percarinatus*, some *Laemanctus longipes*, *L. serratus*, and many polychrotids, while it is short in tropidurids (except *Uranoscodon superciliosus*), phrynosomatids, oplurids (except *O. fierinensis*), and iguanids.

The angular bears the posterior mylohyoid foramen. This foramen usually is positioned well posterior to the superior apex of the coronoid in *Gambelia* (eight of eight *G. copei*, 26 of 29 *G. silus*, 50 of 51 *G. wislizenii*), while it is equidistant with, or anterior to, the superior apex in most *Crotaphytus* (posterior to the superior apex in two of 49 *C. collaris*, three of 15 *C. dickersonae*, two of 17 *C. nebrius*, two of 23 *C. reticulatus*, one of 27 *C. vestigium*). Although most of the outgroup taxa exhibit the condition observed in *Crotaphytus*, the presence of the posterior mylohyoid foramen posterior to the apex of the coronoid in phrynosomatids, some tropidurids, and some polychrotids (Frost and Etheridge, 1989) as well as some oplurids prohibits polarization of this character.

Coronoid (Character 25; Fig. 13, 14).—The angle of the posterolingual process of the coronoid is nearly vertical in *Crotaphytus*, while it extends posteroventrally at an angle of approximately 45 degrees in *G. wislizenii*, *G. copei*, and *G. corona*† (Norell, 1989). *Gambelia silus* may be intermediate in this feature or may approach the conditions observed in *Crotaphytus* or *G. wislizenii–G. copei*. Therefore, *G. silus* was coded as unknown ("?") for this character. Most outgroup taxa have a condition similar to *Crotaphytus* (state 0) or occasionally the intermediate condition usually present in *G. silus*. The outgroup taxa with the *G. wislizenii–G. copei* condition include only *Petrosaurus mearnsi*, *Phrynosoma douglassi*, *P. coronatum*, *Uromastyx*, *Brookesia stumpffi*, and *Chamaeleo kersteni* (chamaeleonines as a whole are variable with respect to this feature). Therefore, the angled posterolingual process of the coronoid (state 1) is considered to be derived and the vertical condition ancestral. Norell (1989) considered this feature to be an unambiguous synapomorphy of *Gambelia*, presumably because he did not examine specimens of *G. silus*.

Surangular (Characters 26–28; Fig. 13–15).—Immediately anterior to the articular facet lies a medially oriented knob-like process here referred to as the medial process. A thin shelf of bone may extend anteriorly between the distal extremity of the medial process and the body of the surangular (Fig. 15). This shelf is usually much more strongly developed in *Gambelia* and, to a lesser degree, *Crotaphytus insularis* than in the remaining *Crotaphytus* species. *Crotaphytus vestigium* is variable with respect to this character with seven of 27 having a shelf present. A lesser amount of variation was observed with a smaller shelf present in *C. bicinctores* (one of 25), *C. collaris* (five of 50), *C. dickersonae* (two of 16), *C. nebrius* (one of 17), and *C. reticulatus* (one of 14). In *Gambelia*, the shelf may entirely fill this space such that its edge may be either straight or, more frequently, convex in shape. The strongly developed condition present in *Gambelia* suggests that it may be a further modification or intensification of the condition observed occasionally in *Crotaphytus*. Thin shelves of bone between the medial process and the ramus of the mandible are present in a small number of iguanian taxa, including *Leiolepis belliana*, *Oplurus cuvieri*, some *Brachylophus fasciatus*, some *Uta stansburiana*, *Urosaurus auriculatus*, *Microlophus grayi*, and most *Phymaturus* taxa (absent only in *P. palluma* and some *P. punae*). The shelves only approached the condition of *Gambelia* in the four *Phymaturus patagonicus* subspecies. This character was coded as a binary character with the absence of a shelf coded as state 0 and its presence as state 1 (taxa with intermediate frequencies coded appropriately). The presence of thin shelves of bone between the medial process of the surangular and the ramus of the mandible is interpreted as the derived state.

An additional process of the surangular may be present immediately anterolateral to the articular facet. In *Crotaphytus*, a large knob-like process is present (here referred to as the lateral process), presumably to provide a large surface area for insertion of the jaw adductor musculature of these lizards. In most *Gambelia*, no obvious process is visible, although in some individuals, a small elevation is present. In the outgroup taxa, a large lateral process is present in *Uromastyx acanthinurus*, *U. microlepis*, *Oplurus fierinensis*, some *Leiocephalus macropus*, *Phrynosoma coronatum*, some *P. douglassi*, some *Uma inornata*, *Urosaurus auriculatus*, the leiosaurs *Pristidactylus*, *Diplolaemus*, and *Leiosaurus*, the para-anoles, and *Polychrus* (although in *Polychrus*, the process is displaced further anteriorly). The lateral process was enlarged to the degree observed in *Crotaphytus* only in *Pristidactylus*, *Diplolaemus*, and *Leiosaurus*. The presence of an enlarged lateral process of the surangular is interpreted as the derived state within Crotaphytidae.

In crotaphytids, a ridge on the dorsolateral surface of the surangular extends between the lateral process and the labial process of the coronoid. This ridge provides a broader area for insertion of M. adductor mandibularis externus on the dorsal surface of the surangular. In *Gambelia*, the ridge is either absent or only weakly developed. In *Crotaphytus*, the ridge and corresponding dorsal shelf are more strongly developed, and in *C. reticulatus*, the ridge is extremely well developed providing a concave area for muscle insertion in adults (Fig. 15). This feature was coded as an unordered multistate character with *Gambelia* given state 0, *Crotaphytus* (except *C. reticulatus*) given state 1, and *C. reticulatus* given state 2. All of the outgroup taxa either lacked this ridge or had a very weakly developed one (state 0), with the possible exception of *Hydrosaurus amboiensis*, in which a ridge is present near the ventrolateral border of the mandible, *Oplurus fierinensis*, and some *Phrynosoma* (*P. asio* and some *P. douglassi* and *P. orbiculare*), in which the ventrolateral portion of the mandible is greatly expanded. The absence of a ridge or the presence of a weakly developed one is considered to be the ancestral state.

Prearticular (Character 29; Fig. 13–15).—Posteriorly, the prearticular bears two large processes that serve as insertion sites for jaw adductor and depressor muscles. The angular process projects ventromedially from a point just below the articular facet, while the retroarticular process projects posteriorly. In *Gambelia*, thin shelves of bone extend between the processes of the posterior portion of the mandible and the ramus of the mandible. One such shelf was discussed above with the surangular. Two additional shelves may also be present, both of which are associated with the angular process. One extends between the angular process and the retroarticular process, while the other extends forward from the angular process to the body of the lower jaw. Shelves of bone that extend between the processes of the mandible and the ramus of the mandible were treated as a single character (see surangular).

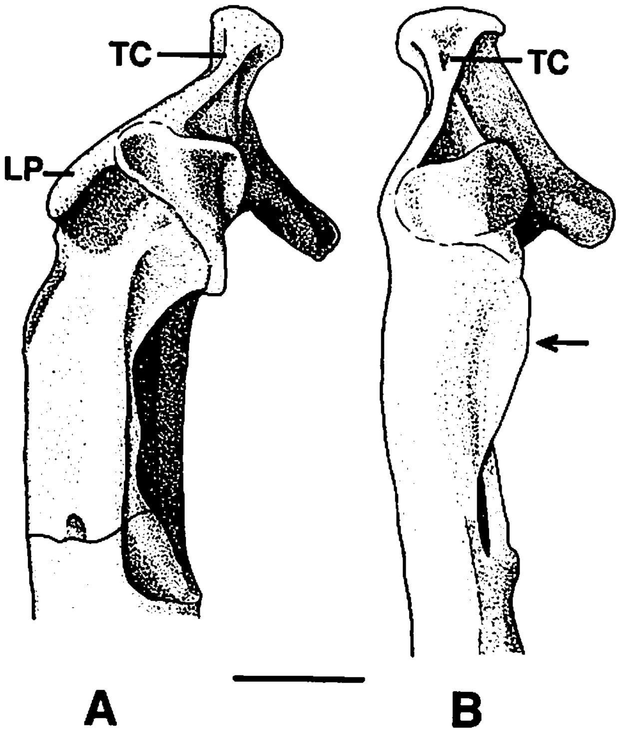

Fig. 15.—Dorsal view of the posterior portion of the right mandible in (A) *Crotaphytus reticulatus* (REE 2912, adult male, SVL = 122 mm) and (B) *Gambelia copei* (REE 2800, adult female, SVL = 123 mm). LP = lateral process, TC = tympanic crest. Arrow indicates the shelf that extends between the medial process and the ramus of the mandible in *Gambelia*. Scale = 3 mm.

The shape of the retroarticular process and its tympanic crest in crotaphytids is distinctive. In dorsal view, the retroarticular process is roughly quadrangular, while in lateral view it is more nearly triangular. The distal terminus of the process is expanded, giving it a bulbous appearance. The tympanic crest is more broadly expanded in *Gambelia* than in *Crotaphytus* (Fig. 15), but was not scored as a separate character state. The tympanic crest in all crotaphytids is robust and its edge expands posteriorly such that at the end of the process, it is nearly as broad as the process itself. Furthermore, the tympanic crest angles posterodorsally and, thus, does not form the lateral border of the retroarticular process as it does in most other iguanian taxa examined (illustrations of the ancestral condition of the tympanic crest can be seen for *Dipsosaurus dorsalis* in de Queiroz, 1987:fig. 29; for *Basiliscus vittatus* and *Corytophanes cristatus* in Lang, 1989:fig. 31; and for *Physignathus cocincinus* in Moody, 1980:fig. 16). The angle of the tympanic crest gives the retroarticular process a twisted appearance. The orientation of the tympanic crest appears to undergo an ontogenetic change from the standard position along the lateral border of the retroarticular process in juveniles to a more posterodorsal orientation in adults. The medial crest of the retroarticular process, discussed by de Queiroz (1987), is only variably present in crotaphytids. A similar posterodorsal curvature of the tympanic crest was observed only in *Oplurus cuvieri* and one *Polychrus acutirostris* (REE 568). Therefore, this condition is interpreted as a synapomorphy for Crotaphytidae.

MISCELLANEOUS FEATURES OF THE HEAD SKELETON

Marginal Teeth (Characters 30, 31; Fig. 8, 11–14).—The marginal teeth of crotaphytids are characteristic of most pleurodont iguanians in that the anterior teeth are conical and the posterior maxillary and dentary teeth are compressed and tricuspid. The dentition of crotaphytids has been described as heterodont or weakly subheterodont (Marx, 1950; Weiner and Smith, 1965) because the teeth sometimes grade from conical to bicuspid then tricuspid (the bicuspid state is often omitted). This transition usually begins further anteriorly in *Crotaphytus* (mean maxillary tooth position $\bar{x} = 8.11$, $n = 152$) and *Gambelia silus* ($\bar{x} = 8.08$, $n = 30$) than in *G. wislizenii* ($\bar{x} = 11.27$, $n = 43$) or *G. copei* ($\bar{x} = 11.13$, $n = 8$), although the ranges overlap extensively. Heterodonty was considered to be more developed in *Gambelia* than *Crotaphytus* by Marx (1950) and Weiner and Smith (1965) and was used as a character to distinguish between the genera. However, Montanucci (1969) found that the degree of heterodonty was indistinguishable between adult *G. wislizenii* and many *C. collaris*, especially juveniles. The degree of cuspation is certainly more pronounced in *Gambelia* than *Crotaphytus* and, despite the ontogenetic variation discussed by Montanucci (1969), this subtle variation could probably be coded into discrete character states. However, degree of cuspation varies continuously within iguanians and this character therefore may be added to the long list of currently unpolarizable differences between *Crotaphytus* and *Gambelia*. As in many iguanian lizards, the number of maxillary and dentary teeth increases ontogenetically, at least early in ontogeny. The number of premaxillary teeth does not increase ontogenetically.

In some individuals of both *Crotaphytus* (Etheridge, 1960; personal observation) and *Gambelia*, the tooth rows of the mandibles and/or maxillae may be doubled for a short distance (two sets of teeth occurring side by side). Although Etheridge (1960) hypothesized that this variation may be restricted to males, it actually occurs in both sexes.

The number of maxillary and dentary teeth tends to be greatest in *Gambelia wislizenii*, *G. copei*, and *Crotaphytus dickersonae* (Tables 3, 4). The large number of teeth in these *Gambelia* is not surprising given the elongate snout that is characteristic of these species. The large number of teeth observed in *C. dickersonae* is the result of very closely spaced dentition. The small number of teeth present in *G. silus* is probably correlated with the truncated snout of this species and may therefore be a plesiomorphic retention. Discrete character states could not be assigned describing numbers of maxillary and dentary teeth. Therefore, this variation was not considered in the phylogenetic analysis.

The number of premaxillary teeth varies within Crotaphytidae (Tables 3, 4). *Gambelia* is characterized by the strong statistical mode of seven premaxillary teeth, while most *Crotaphytus* taxa have a somewhat weaker statistical mode of six. However, *C. dickersonae* and some populations of *C. collaris* (those formerly referred to the subspecies *C. c. baileyi*) have modes of seven. This variation was coded as a multistate character using a step matrix and the Manhattan distance frequency approach (see Appendix 4). This character was not polarized.

All crotaphytids have recurved anterior maxillary and dentary teeth, a condition that is more developed in *Gambelia* than *Crotaphytus*, which have broader, more peg-like teeth (especially evident in *C. reticulatus*). Long, slender, recurved maxillary and dentary teeth, as present in *Gambelia*, were not observed in any of the outgroup taxa and are therefore treated as the derived state.

Palatal Teeth (Characters 32, 33; Fig. 11).—At the base of the pterygoid process of each palatine,

Table 3.—*Tooth count data for* Crotaphytus.

	Premaxillary teeth	Maxillary teeth	Dentary teeth
Crotaphytus:			
antiquus (*n* = 4)			
mean ± SD	5.8 ± 0.50	16.9 ± 0.44	22.0 ± 1.20
range	(5–6)	(15–19)	(21–24)
bicinctores (*n* = 24)			
mean ± SD	6.2 ± 0.53	16.9 ± 0.44	23.0 ± 2.25
range	(5–7)	(15–21)	(18–28)
collaris (*n* = 49)			
mean ± SD	6.2 ± 0.76	17.2 ± 1.78	21.5 ± 2.48
range	(5–8)	(14–22)	(16–26)
dickersonae (*n* = 16)			
mean ± SD	7.1 ± 0.95	20.3 ± 2.60	24.8 ± 3.51
range	(6–9)	(16–25)	(19–31)
grismeri (*n* = 5)			
mean ± SD	6.4 ± 0.89	18.6 ± 1.96	23.1 ± 2.23
range	(6–8)	(16–21)	(19–26)
insularis (*n* = 5)			
mean ± SD	6.0 ± 0.00	18.1 ± 1.60	23.8 ± 1.99
range	(6)	(15–20)	(22–28)
nebrius (*n* = 17)			
mean ± SD	6.2 ± 2.17	18.3 ± 2.17	22.4 ± 2.73
range	(5–7)	(15–23)	(19–30)
reticulatus (*n* = 25)			
mean ± SD	6.0 ± 0.64	17.7 ± 1.69	21.9 ± 1.75
range	(5–7)	(14–21)	(17–25)
vestigium (*n* = 28)			
mean ± SD	6.2 ± 0.39	18.3 ± 1.61	23.3 ± 2.12
range	(6–7)	(15–22)	(19–28)

most crotaphytids have an enlarged ridge that may support palatine teeth. This ridge is usually more developed in *Gambelia* than *Crotaphytus*. Most *Gambelia* (*G. wislizenii*, 39 of 46; *G. copei*, eight of nine; *G. silus*, 17 of 31) have palatine teeth. Within *Crotaphytus*, the palatine ridge is almost always present but the teeth are only variably present (*C. bicinctores*, ten of 24; *C. antiquus*, three of four; *C. collaris*, 19 of 45; *C. dickersonae*, 12 of 16; *C. grismeri*, two of five; *C. nebrius*, 11 of 15; *C. reticulatus*, 17 of 26; *C. vestigium*, ten of 25), although only *C. insularis* (zero of five) always lacked palatine dentition. Among the outgroup taxa examined, palatine teeth are present only in some *Oplurus* (*O. quadrimaculatus*) and most polychrotids (all but *Polychrus*, although palatine teeth are also absent in all

Table 4.—*Tooth count data for* Gambelia.

	Premaxillary teeth	Maxillary teeth	Dentary teeth
Gambelia:			
copei (*n* = 9)			
mean ± SD	7.0 ± 0.00	20.9 ± 1.09	26.2 ± 1.54
range	(7)	(19–23)	(23–29)
silus (*n* = 31)			
mean ± SD	6.6 ± 0.57	17.7 ± 1.46	22.0 ± 1.56
range	(5–7)	(14–20)	(19–25)
wislizenii (*n* = 45)			
mean ± SD	6.9 ± 0.42	19.9 ± 2.26	24.9 ± 2.80
range	(6–8)	(15–24)	(18–31)

anoles except *Chamaeleolis*). Because Frost and Etheridge (1989) found *Polychrus* to be the sister taxon of the anoles, the presence of palatine teeth is considered as the ancestral state for Polychrotidae. Therefore, if palatine teeth are to be considered apomorphic for Crotaphytidae, it must be assumed that Crotaphytidae and Polychrotidae are not sister taxa. Such a relationship was not supported in the analysis of Frost and Etheridge (1989) as depicted in their 12 equally parsimonious unrooted trees. Therefore, palatine teeth are tentatively considered to be apomorphic for Crotaphytidae.

All crotaphytids possess pterygoid teeth on the posteromedial border of the palatine process (Fig. 11). These teeth may form a single row or, late in ontogeny, exist as a patch. During ontogeny, the number of pterygoid teeth clearly increases, although there is not a perfect correlation between number of teeth and SVL and some very large individuals have relatively few teeth. Additional teeth are usually added to the posterior portion of the patch, and in larger individuals, the majority of the teeth are found posteriorly. In some juvenile and most adult *Crotaphytus*, the posterior aspect of the pterygoid tooth row curves laterally away from the interpterygoid vacuity (Fig. 11), while in *Gambelia* the tooth row follows the margin of the vacuity. Polarization of this character is complicated by the absence of pterygoid teeth in the families Phrynosomatidae and Chamaeleonidae and in some *Phymaturus* and *Leiocephalus*. Furthermore, pterygoid teeth are often intraspecifically variable and limited sample sizes for certain outgroup species probably did not allow them to be coded adequately for this character. However, in the remaining outgroup taxa examined, the pterygoid tooth patch was observed to curve posterolaterally only in *Uranoscodon superciliosus*, *Corytophanes percarinatus*, some *C. cristatus*, some *Laemanctus serratus*, *Brachylophus fasciatus*, and *Pristidactylus casuhatiensis* (see de Queiroz, 1987, for additional iguanid taxa with posterolaterally curved pterygoid tooth patches). Therefore, the posterolateral curving of the pterygoid tooth patch was considered to be the derived state within Crotaphytidae.

Scleral Ossicles.—The scleral ossicles are thin, overlapping platelets of bone that form a supportive ring within the anterior portion of the sclera of the eye. De Queiroz (1982) found that most iguanian taxa are characterized by a standard pattern consisting of 14 ossicles, with numbers one, six, and eight positive (overlapping both of the adjacent ossicles), numbers four, seven, and ten negative (overlapped by both of the adjacent ossicles), and the remaining ossicles imbricating (overlapping one of the adjacent ossicles, but itself overlapped by the other). He noted that this pattern is present in *Crotaphytus collaris*, *C. vestigium*, and *Gambelia wislizenii*. I have verified his observations for these species, and report further that the remaining crotaphytid taxa are also characterized by this apparently ancestral iguanian condition. A list of specimens for which the scleral ossicles have been examined is provided in Appendix 7.

Hyoid Apparatus (Characters 34–36; Fig. 16).—A number of differences in the morphology of the hyoid apparatus exist between *Crotaphytus* and *Gambelia*. In *Crotaphytus*, the ceratohyals may be greatly expanded proximally, such that a large hook or process is present (processes absent in one of four *C. antiquus*). Their development is subject to ontogenetic variation and subadults did not have the hook; therefore, the character was scored only from adults. In *Gambelia*, the proximal portion of the ceratohyal may be somewhat compressed; however, well-developed hooks are absent. This character varies extensively in the outgroups and was therefore left unpolarized.

In *Gambelia*, the second ceratobranchials are short, extending posteriorly for about half the length of the ceratohyals and first ceratobranchials, while in *Crotaphytus* they are longer, extending more than two-thirds the length of the ceratohyals and first ceratobranchials (Robison and Tanner, 1962; Fig. 16). The second ceratobranchials of *C. dickersonae* are often particularly long and in adult males usually extend as far posteriorly as do the ceratohyals and first ceratobranchials. However, this was not treated as a separate character state because of continuous variation between the extreme *C. dickersonae* condition and that present in other *Crotaphytus*, particularly in *C. collaris*. The longer second ceratobranchials of *Crotaphytus* may function in the depression of their more strongly developed gular pouch. The outgroups vary continuously in the length of the second ceratobranchials ranging in relative length from very short in *Phymaturus* to extremely elongate in *Polychrus*, the anoles, and *Brachylophus*. Therefore, this character was left unpolarized.

In *Crotaphytus*, the second ceratobranchials are in close contact, although they are not actually fused, whereas in *Gambelia*, they may be widely separated

(Fig. 16). They were separated in one of four *C. antiquus*, in all specimens of *G. copei* and *G. silus*, and in at least ten of 15 *G. wislizenii*. However, in those five specimens of *G. wislizenii* in which the second ceratobranchials were in contact, the contact may have been an artifact of preparation. Separated second ceratobranchials are relatively rare in iguanians and were only observed in *Uta stansburiana*, some *Petrosaurus mearnsi*, *Phrynosoma asio*, some *Uma exsul*, some *Brachylophus fasciatus*, *Phymaturus*, some *Leiolepis belliana*, and *Enyalius bilineatus*. Separated second ceratobranchials was considered to be the derived state within Crotaphytidae. However, this character could not be evaluated in many outgroup taxa because the hyoid apparatus is often damaged in preparation and this polarity assessment should only be considered tentative.

Skull Rugosity (Character 37).—Rugosity of the skull was considered to be a synapomorphy for *Crotaphytus* by Frost and Etheridge (1989). Although rugosities may indeed be found in all *Crotaphytus* taxa (rugosities are not found in *Gambelia*), there is much variation with respect to the ontogenetic period during which rugosities develop. For example, most *C. collaris* develop rugosities as subadults, while *C. bicinctores*, *C. dickersonae*, and *C. nebrius* consistently develop rugosities only after reaching adult size. In *C. grismeri*, *C. insularis*, *C. reticulatus*, and *C. vestigium*, rugosities may be lacking even in large adults. For example, an extremely large *C. vestigium* (REE 2935; SVL = 125 mm) completely lacks skull rugosity, while several much smaller individuals have them. This variation was coded as a binary character with the absence of skull rugosity as state 0, and the presence of skull rugosity at some point in ontogeny as state 1. This character could not be polarized.

Axial Skeleton

Presacral Vertebrae (Character 38).—The presacral vertebrae of crotaphytids are procoelous and have supplemental articular facets, zygosphenes and zygantra, medial to the pre- and postzygapophyses. A large posterodorsally oriented suprazygapophysial process is present on the atlas. Crotaphytids retain the apparently plesiomorphic mode of eight cervical vertebrae and 24 presacral vertebrae, although individuals occasionally have nine cervicals and more frequently may have 23 or 25 total presacrals. Four to seven ventrally keeled intercentra occur between the anteriormost cervical vertebrae and these decrease in size posteriorly.

The zygosphenes and zygantra of all crotaphytid taxa except *Gambelia silus* are weakly to moderately developed, according to the criteria established by Hoffstetter and Gasc (1969) and modified by de Queiroz (1987). In the weak form, the facet of the zygosphene faces dorsolaterally, while in the moderately developed form, the facet faces either laterally or ventrolaterally. The most strongly developed form of zygosphene is characterized by a ventrolaterally facing facet with a notch separating this facet from the prezygapophysis. This condition is approached in four of five *G. silus*, in which either a notch is present or a very thin sheet of transparent bone fills the space. Although notched zygosphenes are present in several of the outgroup taxa, including corytophanids, iguanids exclusive of *Dipsosaurus*, *Uranoscodon superciliosus*, *Polychrus marmoratus*, and some *Enyalius* (*E. boulengeri*, *E. bilineatus*), the condition of *G. silus* is considered to be the derived state within Crotaphytidae.

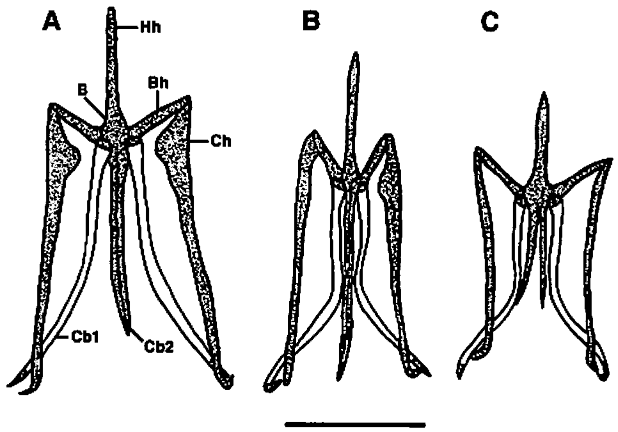

Fig. 16.—Hyoid skeletons of (A) *Crotaphytus collaris* (REE 2952, adult male, SVL = 131 mm), (B) *C. dickersonae* (REE 2905, adult male, SVL = 106 mm), and (C) *Gambelia copei* (REE 2800, adult female, SVL = 123 mm). B = body of hyoid, Bh = Basihyal, Cb1 = first ceratobranchial, Cb2 = second ceratobranchial, Ch = Ceratohyal, Hh = hypohyal. Scale = 10 mm.

Caudal Vertebrae (Characters 39, 40).—The number of caudal vertebrae present in crotaphytids is remarkably consistent with all of the species having between 54 and 63. No gaps were observed suggesting that the number of caudal vertebrae is not phylogenetically informative within Crotaphytidae. Most of the caudal vertebrae bear neural arches, transverse processes, and haemal arches, all of which decrease in size posteriorly and disappear before the caudal terminus. The first haemal arch or rudimentary haemal arch usually occurs between the second and third or third and fourth caudal vertebrae, although it may occasionally lie between the first and second caudal vertebrae. The number of transverse processes is highly variable. Relatively few transverse processes are present in *C. insularis* (14–18, $\bar{x}$ = 16.6), *C. grismeri* (16–22, $\bar{x}$ = 18.0), *G. silus* (14–24+, $\bar{x}$ = 18.0), *G. wislizenii* (13–26, $\bar{x}$ = 18.4), *C. antiquus* (19–22, $\bar{x}$ = 20.3), *C. vestigium* (17–30, $\bar{x}$ = 21.3), *C. bicinctores* (16–26, $\bar{x}$ = 21.9), and *G. copei* (17–26, $\bar{x}$ = 23.3), while an intermediate number is present in *C. dickersonae* (24–35, $\bar{x}$ = 28.6), and a relatively large number are found in *C. reticulatus* (29–38, $\bar{x}$ = 33.4), *C. nebrius* (23–42, $\bar{x}$ = 34.9), and *C. collaris* (27–47, $\bar{x}$ = 37.4). These numbers may be complicated by ontogenetic variation as juveniles tended to have fewer transverse processes than adults. Although the data presented here are suggestive, the extensive interspecific overlap in ranges prevented the assignment of discrete character states for each taxon. Therefore, this variation was not considered in the phylogenetic analysis.

In many iguanian lizards, the transverse processes of the more anterior caudal vertebrae project posterolaterally but abruptly change to an anterolateral orientation over the span of a few vertebrae (Etheridge, 1967). As Etheridge (1967) pointed out, this condition is present in crotaphytids, although in two taxa unavailable to Etheridge at the time, *C. grismeri* (five of five) and *C. insularis* (four of five), this change in orientation usually does not occur. The shift in orientation did not occur in seven of 15 *C. bicinctores*, one of four *C. antiquus*, one of 15 *C. dickersonae*, three of 21 *C. vestigium*, and four of 21 *G. wislizenii*. The ranges and means for the caudal vertebra number at which the shift in orientation of the transverse processes occurs for each taxon follows: *C. antiquus* (8–15, $\bar{x}$ = 10.7), *C. dickersonae* (8–12, $\bar{x}$ = 11.3), *C. insularis* (12), *C. nebrius* (10–17, $\bar{x}$ = 12.5), *C. collaris* (10–18, $\bar{x}$ = 13.3), *G. silus* (13–16, $\bar{x}$ = 14.2), *C. vestigium* (9–22, $\bar{x}$ = 14.3), *G. wislizenii* (13–18, $\bar{x}$ = 15.4), *C. reticulatus* (14–20, $\bar{x}$ = 16.1), *G. copei* (16–23, $\bar{x}$ = 17.1), and *C. bicinctores* (17–23, $\bar{x}$ = 19.9). Again, the extensive interspecific overlap in ranges limits the phylogenetic usefulness of this variation and it was not considered in the phylogenetic analysis.

Adult male *C. bicinctores, C. dickersonae, C. grismeri, C. insularis,* and *C. vestigium* are characterized by the presence of a strongly laterally compressed tail (Fig. 31B, 32A–D). In each of these species, the tail is not only compressed, but relatively taller than in other crotaphytids and this is reflected in the morphology of the caudal vertebrae. The neural and haemal arches are relatively longer and the transverse processes narrower. In the species with strongly compressed tails the neural spines are approximately 2.0–3.0 times longer than the transverse processes while in the remaining species of *Crotaphytus* and in *Gambelia,* the neural spines are shorter than the transverse processes, approximately equal in length, or, in the case of *C. reticulatus,* approximately 1.5 times longer than the transverse processes. The tail of *C. reticulatus* may be weakly laterally compressed. However, the tail is never compressed to the degree observed in the species mentioned above and in some individuals may not be compressed at all. Furthermore, the height of the laterally compressed tail of the other species is enhanced by the presence of large fat bodies on the dorsal and ventral crests of the tail. These large fat bodies are not present in *C. reticulatus* or any other crotaphytid, although I have observed a minute line of fat on the dorsal surface of the tail of one *C. collaris.* Although several anatomical systems have been modified to produce the lateral tail compression of *C. bicinctores, C. dickersonae, C. grismeri, C. insularis,* and *C. vestigium,* these modifications are clearly associated with one complex character and are treated as such in this analysis. Although lateral tail compression occurs in several iguanian families, I have not observed similar fat bodies in the tails of these taxa. Therefore, lateral tail compression with the presence of dorsal and ventral fat bodies is considered to be the derived state within Crotaphytidae.

Autotomic fracture planes of the caudal vertebrae are widespread in squamates and rhynchocephalians and at the level of Iguania certainly represent a plesiomorphic retention (Etheridge, 1967; Hoffstetter and Gasc, 1969). While fracture planes are present in most *Gambelia,* fracture planes are absent from *Crotaphytus* (Etheridge, 1967). Fracture planes were present in five of five *G. silus* and seven of ten *G. copei* (and apparently fused in the remaining three). Fracture planes were present in 19 of 23 *G. wislizenii;* however, the four that lacked them were the only four specimens available from Isla Tiburon and, thus, may represent a derived feature for this insular population. Many iguanian taxa lack autotomic fracture planes, including the hoplocercid *Hoplocercus,* the phrynosomatid *Phrynosoma,* some tropidurids of the genus *Tropidurus,* the polychrotids *Phenacosaurus, Chamaeleolis, Leiosaurus, Polychrus, Urostrophus, Anisolepis, Chamaelinorops,* and some *Enyalius* and *Anolis,* the corytophanids *Corytophanes* and *Laemanctus,* the iguanids *Iguana delicatissima, Conolophus, Amblyrhynchus,* and *Brachylophus,* and all chamaeleonids except occasional *Uromastyx* (Etheridge, 1967; de Queiroz, 1987; Frost and Etheridge, 1989; R. Etheridge, personal communication, 1993). Thus, it is most parsimonious to assume that autotomic fracture planes were present in the common ancestors of the families Opluridae, Hoplocercidae, Iguanidae, Phrynosomatidae, and Tropiduridae, given the phylogenetic relationships that have been proposed for these groups (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Norell and de Queiroz, 1991; Frost, 1992). The polarity of this character is equivocal for Corytophanidae and Polychrotidae (given the relationships proposed by Frost and Etheridge, 1989). The absence of fracture planes is known to be the ancestral condition only with respect to the family Chamaeleonidae. Although this character cannot be unequivocally polarized given the outgroup uncertainties, I have tentatively coded the absence of autotomic fracture planes as the derived state.

Etheridge (1967) mentioned that iguanians with the autotomic version of the type one iguanid (*senso lato*) vertebral pattern (vertebrae with single transverse processes and fracture planes, when present, that pass posterior to the transverse process), of which *Gambelia* is an example, usually have between five and 15 nonautotomic vertebrae that precede the first autotomic vertebra. *Gambelia* generally fits this pattern with the first fracture plane occurring in *G. wislizenii* somewhere between the 14th and 22nd vertebrae, in *G. copei* between the 18th and 21st vertebrae, and in *G. silus* between the 13th and 15th vertebrae.

Ribs (Character 41).—Crotaphytids are characterized by a generally plesiomorphic complement of ribs, although phylogenetically informative variation is present. As in other iguanians, most of the ribs have a bony dorsal portion and a cartilaginous ventral portion, the inscriptional rib, that may either connect the bony portion with the sternum or xiphisternum or end free. The first rib-bearing cervical vertebra is usually the fourth, although the third vertebra supports ribs in numerous individuals, and in a few, the second vertebra supports ribs. Thus, there are usually five cervical ribs, although six or seven are not uncommon. The cervical ribs are followed by four sternal ribs that connect the vertebral column to the posterolateral border of the sternum (only three sternal ribs present in one of four *C. antiquus*). The sternal ribs are followed by either one (*Gambelia*) or two (*Crotaphytus*) xiphisternal ribs that connect the vertebral column with the xiphisternum. Finally, there may be a series of post-xiphisternal ribs that end freely. The ribs rapidly decrease in length posteriorly to a width roughly equal to that of the sacral pleuropophyses. The terminal presacral ribs are often smaller than those immediately anterior to them and are very rarely fused to the vertebra.

Three xiphisternal patterns were observed and two of these appear to be quite consistent. *Crotaphytus* has a pattern of two xiphisternal ribs with an occasional free xiphisternal rod. *Gambelia* have just one xiphisternal rib and one free xiphisternal rod that curves anteromedially. Variation was observed in two specimens of *Crotaphytus* (*C. bicinctores,* REE 2934; *C. collaris,* REE 2948) and two specimens of *Gambelia* (*G. silus,* CAS 22742; *G. wislizenii,* REE 2918). Both *Crotaphytus* specimens had the condition characteristic of *Gambelia,* although REE 2934 varied on one side only. The apparently anomalous specimens of *G. silus* and *G. wislizenii* had two xiphisternal ribs plus a free xiphisternal rod, a condition observed infrequently in *Crotaphytus.* Etheridge (1959) found two xiphisternal ribs to be present in oplurids, corytophanids, iguanids, hoplocercids, polychrotids, tropidurids (with the exception of *Phymaturus* and *Uracentron*), and phrynosomatids (except *Phrynosoma,,* which have no xiphisternal ribs, and *Callisaurus,,* with three). Frost (1992) listed several additional species of *Tropidurus* and one *Microlophus* with three xiphisternal ribs. In chamaeleonids exclusive of chamaeleonines, one xiphisternal rib is the common condition and is present in the presumably basal lineages of agaminae (*Physignathus, Hydrosaurus*), while the absence of xiphisternal ribs were characteristic of *Uromastyx* and *Leiolepis* (Moody, 1980). In the few chamaeleonines that I have examined (*Chamaeleo senegalensis, C. johnstoni*), two xiphisternal ribs were present, although variation within chamaeleonines seems likely. Because two xiphisternal ribs is clearly the ancestral condition in all of the iguanian families except Chamaeleonidae, the presence of two xiphisternal ribs is assumed to be the ancestral state within Crotaphytidae. Therefore, two xiphisternal ribs was coded as state 0 and that of a single xiphisternal rib as state 1.

The shape of the xiphisternal rod of *Gambelia* is similar to that described in *Tropidurus semitaeniatus* (Frost, 1992) in that the free end of the cartilaginous rod curves anteromedially, crossing superficially to the xiphisternal rib and posteriormost sternal ribs. The posterior xiphisternal rod serves as the origin for nearly the entire posterior portion of M. pectoralis major, although it does not serve as the entire origin as in *T. semitaeniatus.* Regardless of whether the posteriormost xiphisternal cartilage ends freely or is continuous with a bony rib, it appears to serve as the site of origin for a portion of M. pectoralis major. This appears to be the case even in those taxa that have extremely short cartilaginous protuberances projecting posteriorly from a second xiphisternal rib, for example *G. silus* and certain phrynosomatids (Etheridge, 1964).

PECTORAL GIRDLE

Suprascapulae (Character 42).—The suprascapulae are composed entirely of calcified cartilage and lie dorsal to the scapulae. In *Crotaphytus* and some *Gambelia,* a deep notch is present in the anterior margin of the suprascapula giving it the appearance of a hook. This notch is usually present in *Crotaphytus* and variably present in *Gambelia* (five of 23 *wislizenii,* one of seven *copei,* one of five *G. silus*). Most of the outgroup taxa lack a strongly developed notch in the suprascapula (present in one of one *Corytophanes hernandezi* and four of four *Uma scoparia*). Therefore, the presence of a suprascapular notch is treated as the derived state.

Scapulae, Coracoids, and Epicoracoids (Characters 43, 44).—In crotaphytids, the posterior coracoid fenestrae are nearly always present (absent on one side only in one of five specimens of *C. insularis,* and on one side only in one of 23 *G. wislizenii*). In *C. reticulatus,* the posterior coracoid fenestrae were observed to be absent in three of nine individuals. Furthermore, they were either proportionally smaller or present unilaterally in the remaining large specimens, suggesting that the fenestrae are lost late in ontogeny in this species. Posterior coracoid fenestrae are absent in the great majority of iguanians and among the outgroup taxa are present in *Uromastyx, Liolaemus,* Stenocercini, Tropidurini, iguanids exclusive of *Dipsosaurus* and *Brachylophus,* para-anoles, *Enyalius, Pristidactylus, Leiosaurus,* and *Diplolaemus* (Savage, 1958; Etheridge, 1959; Moody, 1980; de Queiroz, 1987; Frost and Etheridge, 1989). The weakly developed posterior coracoid fenestrae of the latter three taxa were considered by Frost and Etheridge (1989) to represent a separate character state. The presence of posterior coracoid fenestrae are considered to be the derived state and may represent a synapomorphy for Crotaphytidae. The ontogenetic loss of the posterior coracoid fenestrae in *C. reticulatus* may represent an autapomorphy for the species. However, additional osteological material is required to evaluate this potentially distinct character state and it was not treated as such in the phylogenetic analysis.

In *Gambelia,* a calcified extension of the epicoracoid cartilage forms the anterior border of the scapular fenestra. The anterior border of the scapular fenestra was either absent or incomplete in all of the *Crotaphytus* specimens examined except three of 21 *C. bicinctores,* one of 12 *C. collaris,* one of five *C. grismeri,* one of five *C. insularis,* and three of 21 *C. vestigium.* However, in all of these specimens except two of the three *C. vestigium* and the one *C. collaris,* the border of the fenestra was not completed by calcified cartilage, but rather by a thin sheet of bone or connective tissue. In adult *C. reticulatus,* the calcified cartilage extends dorsally from the ventral border of the scapular fenestra approximately half way to the dorsal border of the fenestra, a condition that may represent an intermediate step between the condition observed in *Gambelia* and that observed in most other *Crotaphytus.* Because the cartilage was present in 34 of 35 specimens of *Gambelia* examined, it seems unlikely that the variation observed was an artifact of preparation. Character polarity could not be evaluated in many of the outgroup taxa because they lack scapular fenestrae, including Chamaeleonidae, Polychrotidae (variable in *Polychrus*), Corytophanidae, Liolaeminae, Hoplocercidae (except *Enyalioides laticeps*), *Petrosaurus, Uta,* and *Urosaurus* (Frost and Etheridge, 1989). In those outgroup taxa that have scapular fenestrae, most have the calcified cartilage borders, including phrynosomatids (except *P. orbiculare*), hoplocercids, oplurids, iguanids, tropidurids (*Leiocephalus* and *Uranoscodon*), and *Hydrosaurus amboiensis* (other agamines lack scapular fenestrae [Frost and Etheridge, 1989]). Therefore, the absence of a calcified cartilage anterior border of the scapular fenestra is tentatively coded as the derived condition.

Clavicles (Character 45).—In *Gambelia*, the clavicles usually (all *Gambelia* except two of 23 *G. wislizenii*) bear extensive fenestrations. Fenestrations were also present in all *Crotaphytus reticulatus* examined, although Montanucci (1969) found that they were absent in six of the 14 specimens he examined. These fenestrations were absent in all 39 *C. collaris* examined, as well as in the 14 *C. nebrius* and five *C. insularis* examined. However, in the remaining species of *Crotaphytus*, there was much variability in this character with four of 21 *C. bicinctores*, two of four *C. antiquus*, five of 16 *C. dickersonae*, three of five *C. grismeri*, and two of 21 *C. vestigium* having fenestrated clavicles. Although Weiner and Smith (1965) noted that clavicular fenestrations were absent in the 54 specimens of *C. collaris* they examined, Robison and Tanner (1962) observed them in 20 percent of their specimens (although they included specimens of the yet-to-be-described *C. bicinctores* in their sample, which at the time was considered to be *C. c. baileyi*) and Montanucci (1969) observed them in one of 45 specimens collected from Kansas and Oklahoma. Thus, clavicular fenestrations, although uncommon, are occasionally present in *C. collaris* and it seems likely that additional specimens will reveal their presence in *C. nebrius* and *C. insularis* as well. Clavicular fenestrations are rare in the basal lineages of the outgroup taxa, being found only in *Basiliscus*, *Laemanctus*, some *Corytophanes hernandezi* (REE 1800, SDSNH 68090, although considered absent from this species by Lang, 1989), some *Uma inornata*, *Ctenoblepharys adspersus*, some *Leiolepis belliana*, *Physignathus concincinus*, some *P. lesueurii*, and *Enyalius brasiliensis*. Therefore, the presence of clavicular fenestrations is considered to be the derived state.

Interclavicle.—The interclavicle is an unpaired median element that lies along the ventral margin of the pectoral girdle. It varies extensively in form, although it usually is in the shape of an anchor or arrow. Lateral processes, present anteriorly, are in close contact with the proximal ends of the clavicles, while a long, narrow posterior process is bordered laterally by the epicoracoid cartilages and the sternum. In most *Crotaphytus* and some *Gambelia*, the interclavicle expands laterally becoming diamond-shaped just anterior to the sternum. Although Weiner and Smith (1965) considered this character to be phylogenetically informative, there is continuous variation in this feature and it was not included in the phylogenetic analysis.

Sternum and Xiphisterna.—The sternum is a median, diamond-shaped element composed entirely of calcified cartilage. Anterolaterally, the sternum thickens, forming grooves into which fit the epicoracoid cartilages. These tongue-in-groove joints allow for extensive mobility of the pectoral girdle elements during locomotion (Jenkins and Goslow, 1983). The sternum also articulates medially with the posterior process of the interclavicle. In the center of the sternum there may be a fontanelle that, when present, is usually invaded by the interclavicle. Posterolaterally, the sternum bears four or five facets that serve as attachment points for the sternal and xiphisternal ribs and the postxiphisternal rods. The posteriormost facets (those that give rise to the xiphisternal ribs) are separated slightly more widely in eastern *Crotaphytus collaris* than in other crotaphytids. A similar, albeit more extreme, condition is observed in *Sauromalus* (de Queiroz, 1987). This may be related to the more depressed habitus of eastern *C. collaris* and their greater propensity for crevice dwelling. This condition was not coded as a character. Weiner and Smith (1965) noted that the sternum of *Crotaphytus* is broader and shorter than in *Gambelia*. Although there does appear to be a trend in this direction, this character appears to vary continuously and was not included in the phylogenetic portion of this analysis. No phylogenetically informative variation was discovered in the sternum (but see above section titled "Ribs" for discussion of xiphisternal rib variation).

PELVIC GIRDLE

Illium and Pubis (Character 46).—In *Gambelia*, the iliac blades are robust and roughly cylindrical at their distal termini, while in *Crotaphytus*, they are usually laterally compressed. However, in some *C. collaris* (primarily those formerly referred to *C. c. collaris*), they may approach the cylindrical condition observed in *Gambelia*. The outgroup taxa are extremely variable with respect to this character and it could not be polarized.

Weiner and Smith (1965) discuss ventrolateral curvature of the pubes and the angle at which the two halves of the pelvic girdle meet. There does not appear to be consistent interspecific variation in either of these features (in fact, I am unaware of any ventrolateral curvature of the pubes, although they

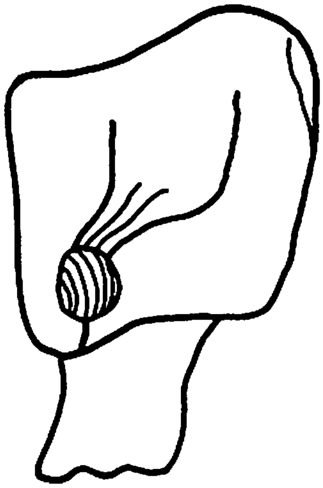

Fig. 17.—Ventral view of the fifth metatarsal bone of *Crotaphytus collaris* showing the contact of the medial and lateral plantar tubercles forming an arch (redrawn from Snyder, 1954).

may be referring to ventromedial curvature). They may have been referring to the presence of a proportionally shorter and broader pelvic girdle in eastern populations of *Crotaphytus collaris* (the only representative of the "collariform" group that they examined) than in other *Crotaphytus* species or *Gambelia*. This difference appears to be related, at least in part, to modification of the pubic rami, which are nearly transverse in orientation, rather than acutely angled anteriorly. However, the condition in the remaining populations of *C. collaris* (formerly referred to *C. c. fuscus*, *C. c. baileyi*, and *C. c. auriceps*) appears to be intermediate in each of these features. Coding of this variation is further complicated by individual variation in pelvic girdle structure, such that some individuals approach the eastern *C. collaris* condition, while others approach the condition of other *Crotaphytus* species. Short, broad pelvic girdles are often observed in crevice-dwelling species (e.g., *Sauromalus*) and the relatively short, broad, pelvic girdles of eastern *C. collaris* may be related to the crevice-dwelling behavior observed in these lizards.

LIMBS

(Character 47; Fig. 17)

On the plantar surface of the fifth metatarsal are two large tubercles termed the medial and lateral plantar tubercles by Robinson (1975). These tubercles serve as attachment points for the tendons of M. gastrocnemius. In the majority of iguanian species, a groove runs between the two tubercles and a tendon of M. flexor digitorum longus passes within it (Robinson, 1975). In *Crotaphytus*, the medial plantar tubercle usually curves laterally such that it contacts the lateral plantar tubercle forming a complete arch (Fig. 17), through which passes the tendon of M. flexor digitorum longus (noted and figured by Snyder, 1954). The contact of the tubercles is usually extensive and in some individuals, the tubercles may fuse completely. The arch condition was absent in the entire available series of *Gambelia* (41 specimens) and, in adults, it was always present in the 20 *C. bicinctores*, four *C. antiquus*, 12 *C. dickersonae*, five *C. grismeri*, and 22 *C. vestigium* examined. It was complete on at least one pes in 28 of 36 *C. collaris*, three of five *C. insularis*, 11 of 12 *C. nebrius*, and six of seven *C. reticulatus*. The majority of specimens that lacked the complete arch were juveniles, and in most cases the gap between the medial and lateral plantar tubercles was narrow. Therefore, this character was scored only for adults. Among the outgroup taxa examined, the arched form of the medial and lateral plantar tubercles was present only in the phrynosomatid sand lizards (*Uma*, *Callisaurus*, *Cophosaurus*, and *Holbrookia*). This feature appears to represent a synapomorphy for *Crotaphytus*, as well as providing additional character support for the monophyly of the phrynosomatid sand lizards.

The hindlimb of *Crotaphytus* is much longer than that of *Gambelia* of similar SVL. A relatively long hindlimb is typical of lizard species that utilize bipedal locomotion (Snyder, 1952, 1954, 1962), although agamines provide an interesting exception. Much of the variation in hindlimb length between *Crotaphytus* and *Gambelia* is realized in the longer crus of the former, while the pes appears to be of relatively similar length. Although a greater relative hindlimb length appears to be a derived characteristic of *Crotaphytus*, there is great variation in the outgroup taxa and this feature was not included in the phylogenetic analysis.

SQUAMATION

The dorsal body squamation of *Crotaphytus* and *Gambelia* is remarkably similar in that both genera are characterized by relatively undifferentiated head scales and fine homogeneous dorsal body squamation. However, despite many similarities in scale patterns and scale sizes on the various regions of the body, phylogenetically useful variation in squamation exists. A more detailed description of the squamation of crotaphytids is provided in the taxonomic accounts of the family, genera, and species.

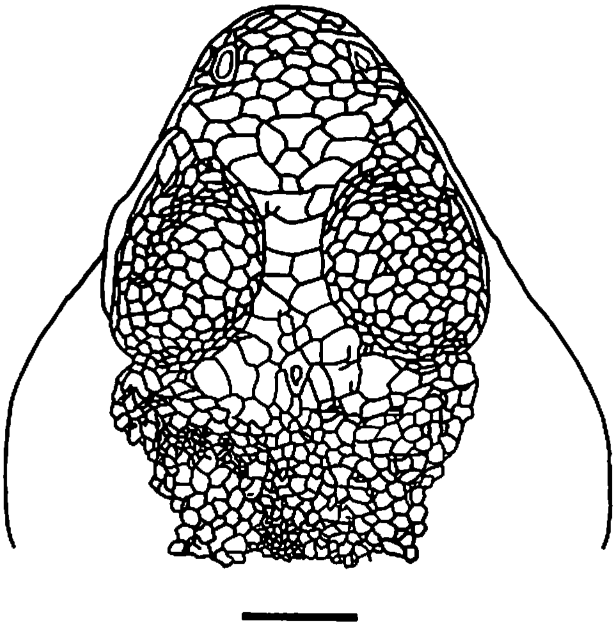

Fig. 18.—Squamation of the dorsal portion of the head of *Crotaphytus collaris* (USNM 17183, adult male). Scale = 5 mm.

Rostral Scale (Character 48).—In all crotaphytids except *Crotaphytus dickersonae*, the rostral scale is approximately four times wider than high. In *C. dickersonae*, the rostral is less elongate and approximately two times wider than high. There is much variation in the outgroups, although most taxa have a rostral that is much wider than high. Consequently, this character was left unpolarized.

Supraorbital Semicircles (Character 49; Fig. 18, 19).—*Crotaphytus* have supraorbital semicircles composed of scales that are much larger than the adjacent supraoculars. In *Gambelia*, obvious supraorbital semicircles are absent, with the supraoculars tending to grade into the frontal series. The outgroups vary considerably in the presence of discrete supraorbital semicircles. They are present in all oplurids and polychrotids examined (except *Chamaeleolis*), and variable within the remaining families. Within Hoplocercidae, they are absent in *Enyalioides laticeps*, but present in *E. praestabilis* and *E. oshaugnessyi*. Within Phrynosomatidae, they are present in *Petrosaurus* and the *Sceloporus* group, *Uma notata*, *U. scoparia*, and *U. inornata*, but absent in *Phrynosoma* and *Uma exsul*. In tropidurids, they are present in some *Phymaturus patagonicus*, *Leiocephalus*, *Liolaemus*, Stenocercini, basal Tropidurini (except *Uranoscodon superciliosus*), and absent in *Ctenoblepharys adspersus*, most *Phymaturus*, and *Uranoscodon superciliosus*. In iguanids, they are present in *Dipsosaurus*, absent in *Brachylophus fasciatus*, and generally absent in the remaining taxa. In chamaeleonids, they are absent in *Hydrosaurus pustulatus*, *Leiolepis belliana*, *Uromastyx loricatus*, and *U. ocellatus*, variable in *U. geyrii*, *U. microlepis*, and *U. acanthinurus*, and present in *U. aegypticus*, *U. asmussi*, *U. hardwickii*, *U. macfadyeni*, *U. philbyi*, and *U. thomasi*. In corytophanids, they are present in *Basiliscus plumifrons*, *B. vitattus*, *Corytophanes hernandezi*, absent in *C. cristatus* and *C. percarinatus*, and variable in *Laemanctus*. Because of this extensive variation, this character was left unpolarized.

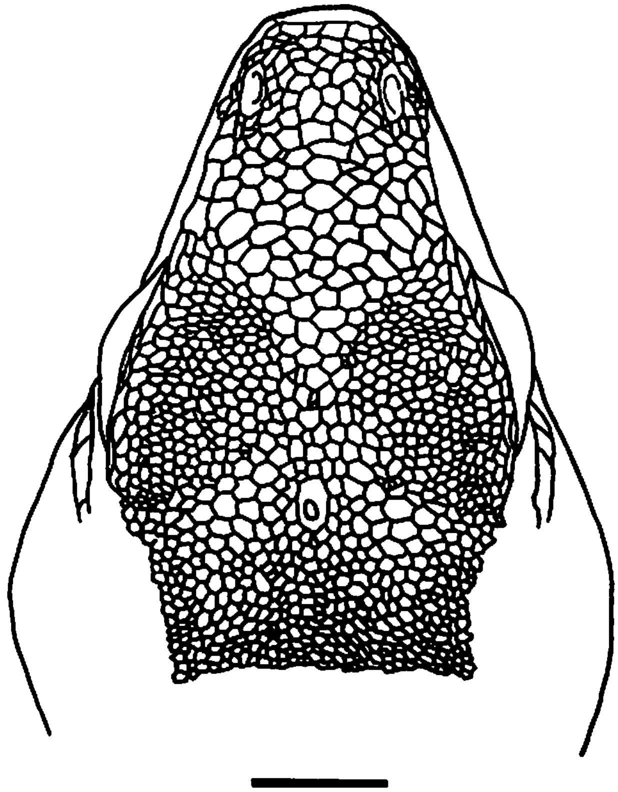

Fig. 19.—Squamation of the dorsal portion of the head of *Gambelia wislizenii* (SDSNH 68662, adult female). Scale = 5 mm.

Suboculars (Character 50; Fig. 20, 21).—In *Crotaphytus*, the suboculars are subquadrate, with the third scale occasionally larger than the others, whereas in *Gambelia*, the second subocular is four to five times larger than the others. Assessing polarity of this feature is difficult because both states are widespread within the Iguania. At least one subocular is much longer than the others in phrynosomatids except *Phrynosoma*, the oplurids *Oplurus*

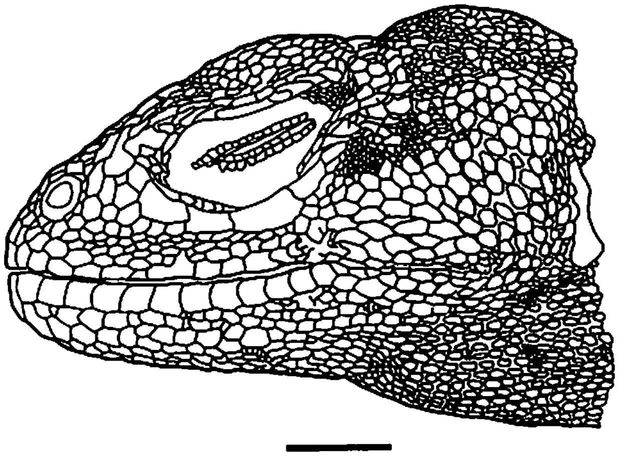

Fig. 20.—Squamation of the lateral portion of the head of *Crotaphytus collaris* (USNM 17183, adult male). Scale = 5 mm.

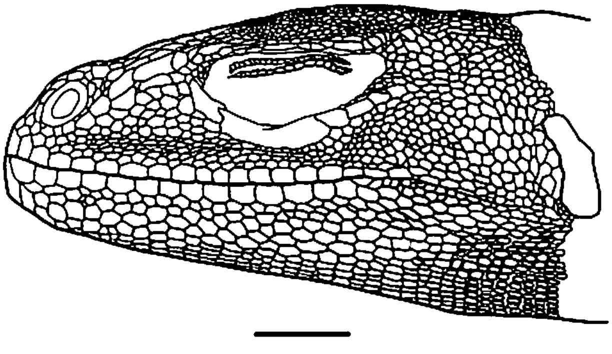

Fig. 21.—Squamation of the lateral portion of the head of *Gambelia wislizenii* (SDSNH 68662, adult female). Scale = 5 mm.

saxicola, O. fierinensis, and *O. quadrimaculatus,* the chamaeleonid *Leiolepis belliana,* the tropidurids *Phymaturus patagonicus, Leiocephalus, Liolaemus,* Stenocercini, *Microlophus, Plesiomicrolophus,* and all but terminal *Tropidurus* (Frost, 1992), the iguanid *Dipsosaurus,* and the polychrotids *Anisolepis, Pristidactylus,* and *Enyalius bilineatus.* Multiple subequal suboculars are present in the oplurids *Oplurus cyclurus, O. cuvieri,* and *Chalaradon,* the chamaeleonids *Uromastyx* and *Hydrosaurus pustulatus,* hoplocercids, the tropidurids *Phymaturus punae, P. palluma, Ctenoblepharys,* and *Uranoscodon superciliosus,* the polychrotids *Urostrophus, Polychrus, Phenacosaurus, Chamaeleolis, Anolis,* and *Enyalius* (except *E. bilineatus*), iguanids (except *Dipsosaurus*), and corytophanids. An elongate subocular appears to be the ancestral state in Phrynosomatidae, Tropiduridae, and Opluridae, and equivocal in Iguanidae, and Polychrotidae. The presence of subequal suboculars is the ancestral state for Corytophanidae, Hoplocercidae, and Chamaeleonidae. Therefore, this character could not be polarized.

Terminal Supradigital Scales (Character 51).—In *Gambelia, C. collaris,* and *C. reticulatus,* the terminal supradigital scales nearly always lie flat against the dorsal surface of the claws. In the remaining *Crotaphytus,* the terminal supradigitals project dorsally such that each is elevated from the claw. A similar elevated condition occurs occasionally in various iguanians including the phrynosomatids *Petrosaurus, Uta stansburiana* (three of four), *U. palmeri* (one of four), and *Uta squamata* (one of three), the tropidurids *Plesiomicrolophus koepkeorum* (one of four), *Microlophus grayi* (one of four), *M. theresioides* (one of four), *M. tigris* (one of four), and *M. stolzmanni* (three of four), and the hoplocercid *Enyalioides laticeps* (one of five). Despite this variation, the presence of elevated terminal supradigital scales is most parsimoniously considered to be the derived state.

Femoral Pores (Characters 52, 53; Fig. 22, 23).—In *Gambelia,* the femoral pores extend distally at least to the inferior angle of the knee. The femoral pore series of *G. silus* usually just reaches this point, while the femoral pore series of *G. wislizenii* and *G. copei* almost always extend beyond and may even arch posteriorly onto the lower leg. The femoral pore series of *Crotaphytus* does not reach the inferior angle of the knee and usually terminates well proximal to this point.

Polarization of this character is complicated by the absence of femoral pores in the Tropiduridae, Opluridae, and Corytophanidae. However, in the remaining outgroups, the femoral pore series always terminates before reaching the inferior angle of the knee (*Phrynosoma coronatum* is variable with respect to this character). Therefore, the condition observed in *Gambelia* is interpreted as the derived state.

In *Gambelia wislizenii* and *G. copei,* the femoral pores of females are large and contain substantial quantities of exudate, although the pores are usually slightly larger in males. In *G. silus, Crotaphytus,* and all of the outgroup taxa examined that have femoral pores except *Enyalioides laticeps,* they are much larger and fuller in males than in females and, indeed, in females the pores may be devoid of exudate. Therefore, the condition observed in *G. wislizenii* and *G. copei* is considered to be the derived state.

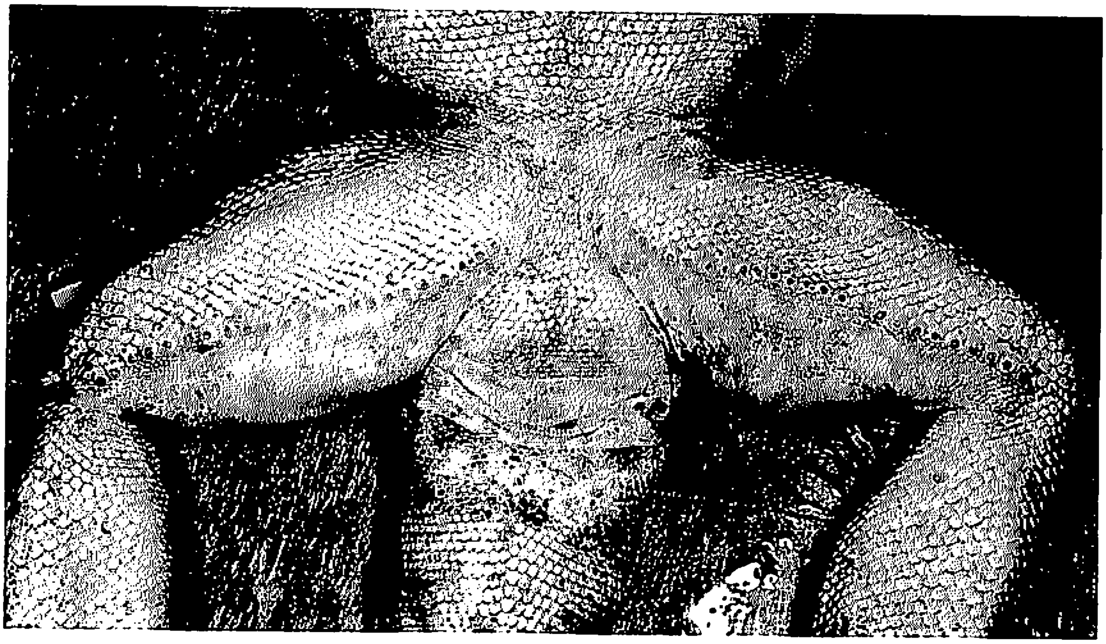

Fig. 22.—Ventral view of *Gambelia wislizenii* (TNHC 33200) showing the femoral pore series extending beyond the angle of the knee.

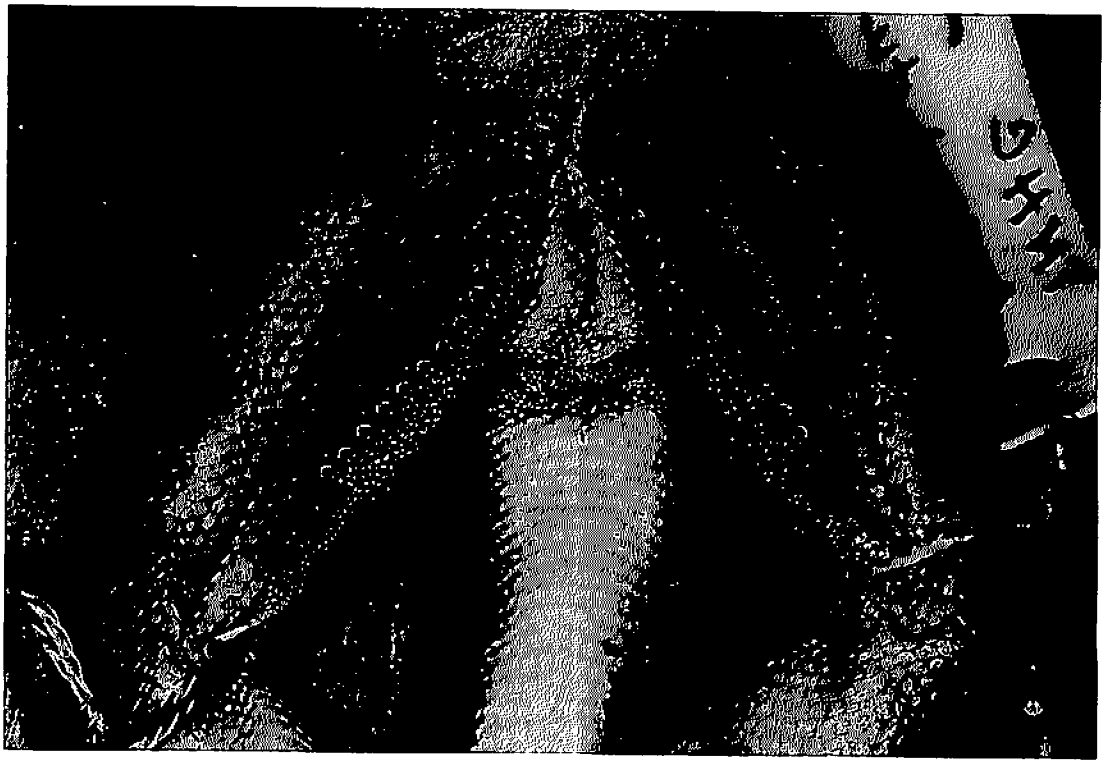

Fig. 23.—Ventral view of *Crotaphytus reticulatus* (TNHC 28364) showing the jet black femoral pores present in males. AGF = antegular fold, GF = gular fold.

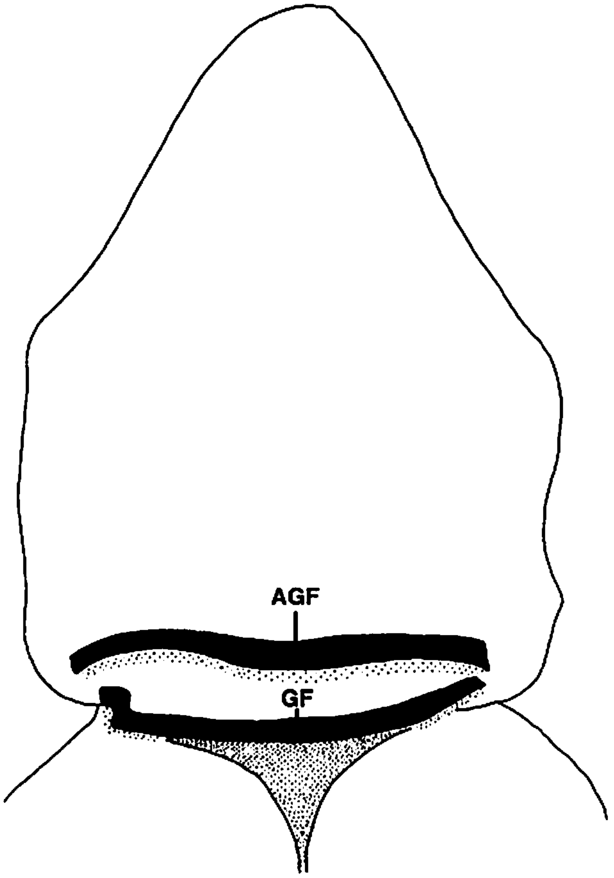

Fig. 24.—Ventral view of the neck folds of *Crotaphytus reticulatus* (EL 3250). Fold terminology follows Frost (1992). AGF = antegular fold, GF = gular fold.

Postanal Scales.—In some iguanian lizards, males can be differentiated from females by the presence of enlarged postanal scales. Within Crotaphytidae, the postanal scales are enlarged in all male *Gambelia,* as well as *C. grismeri, Crotaphytus nebrius,* and most *C. bicinctores* and *C. collaris.* The condition of the postanal scales is more variable in *C. vestigium* and *C. insularis,* with roughly equal proportions of males having large or only slightly enlarged scales. The postanal scales are not enlarged or are only slightly enlarged in *C. antiquus, C. reticulatus,* and *C. dickersonae,* although they may be larger than in females. Attempts to code this character were prohibited by continuous variation in the size of the postanal scales in *C. bicinctores, C. collaris, C. dickersonae, C. insularis, C. reticulatus,* and *C. vestigium.* Furthermore, this character could not be polarized as enlarged postanal scales are present in phrynosomatids, oplurids, many anoles (*Chamaeleolis chamaeleonides, Phenacosaurus,* and most *Anolis*), and some *Leiocephalus* (although Pregill [1992] found that enlarged postanal scales were derived within the genus).

Tail Skin (Character 54).—In all crotaphytids, the skin of the tail is relatively weakly adherent to the underlying musculature such that the skin can be removed easily. This condition contrasts strongly with that observed in most iguanians with fracture planes, such as *Dipsosaurus, Sceloporus,* and *Oplurus,* in which the skin is bound to the underlying musculature by connective tissue and is nearly impossible to remove in one piece. This condition is more strongly developed in *Crotaphytus* than in *Gambelia,* such that in the former, the skin of the posterior 40–50 mm of the tail easily slips off. Loosely adherent skin that is easily removed from the terminal portion of the tail appears to be unusual if not unique among iguanians and is therefore considered to be the derived state (1) in this analysis.

POCKETS AND FOLDS

Crotaphytids, like many fine-scaled iguanian lizards, have extensive lateral neck and gular folding. Both *Crotaphytus* and *Gambelia* share a standard complement of folds that includes gular, antegular, antehumeral, postauricular, longitudinal neck, and supra-auricular folds (terminology follows Frost, 1992). None of these folds are unique to Crotaphytidae and most are similar to folds present in a wide range of iguanian lizards. For example, the gular fold is well developed, enclosing a region of reduced squamation, and is continuous with the antehumeral fold. Also, the antegular fold is continuous with the oblique neck fold. However, phylogenetically informative variation does occur in the folds. As is the case with most fine-scaled species, additional folds are often present with varying degrees of consistency. Thus, I have referred to the above-mentioned complement of folds as the standard pattern and will restrict the discussion to this series.

Gular Fold (Character 55; Fig. 24–27).—The gular fold of *Crotaphytus* differs from that of *Gambelia* in that there is a pair of skin folds that separate from the gular fold and project posteromedially. These folds, which may be ventromedial continuations of the antehumeral folds (R. Etheridge, personal communication, 1993) usually meet midventrally and form a single longitudinally oriented midventral fold that extends posteriorly for a short distance. In the triangular-shaped region between the folds, the scales are reduced in size. In *Gambelia,* a pair of similar

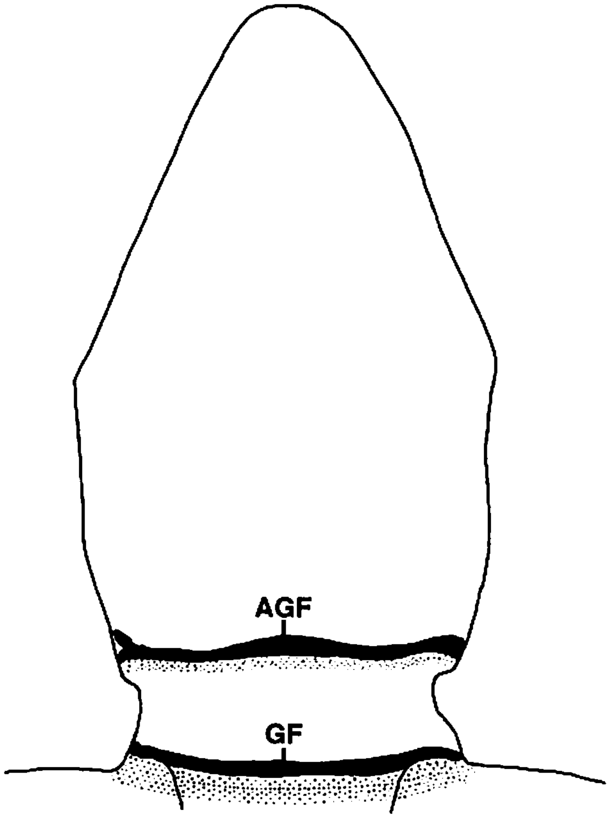

Fig. 25.—Ventral view of the neck folds of *Gambelia wislizenii* (SDSNH 68663). Fold terminology follows Frost (1992). AGF = antegular fold, GF = gular fold.

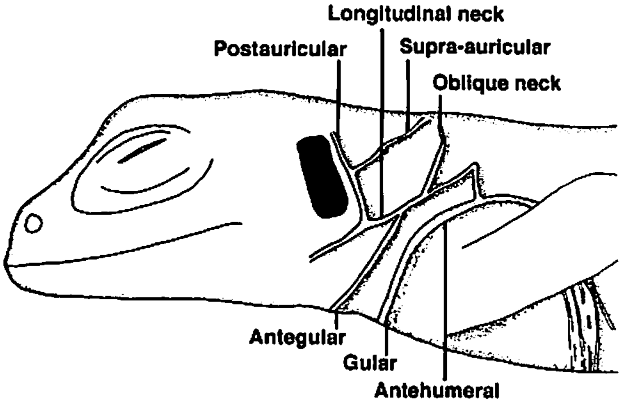

Fig. 26.—Lateral view of the neck folds of *Crotaphytus reticulatus* (EL 3250). Fold terminology follows Frost (1992).

folds may occur; however, they are shorter and appear near the lateral borders of the gular fold. As a result, the area of reduced squamation seen in *Gambelia* takes the form of a uniform band that extends across the width of the gular fold. Those outgroup taxa with gular folds examined here display both conditions of the fold with phrynosomatids, the oplurid *Chalaradon madagascariensis*, chamaeleonids (except *Hydrosaurus pustulatus*), the corytophanids *Basiliscus vittatus* and *Laemanctus*, the hoplocercid *Enyalioides laticeps* (four of five), and polychrotids displaying the *Gambelia* form, and the hoplocercids *Enyalioides praestabilis* and *E. oshaugnessyi*, the corytophanid *Basiliscus plumifrons*, the oplurid genus *Oplurus* (*O. fierinensis* and *O. saxicolus* variable), and the iguanid *Dipsosaurus* displaying the *Crotaphytus* form. Most tropidurids have incomplete gular folds or lack them altogether; thus, the evaluation of this character for Tropiduridae is difficult. *Uranoscodon superciliosus*, which has a complete gular fold, displays the *Gambelia* form. The only other species within Tropidurini with complete gular folds are *Tropidurus azureum*, *T. flaviceps*, and *T. plica* (Frost, 1992), species far removed from the basal lineages of the clade, and, thus, unable to shed light on this polarity decision. Because of ambiguity in the outgroup taxa, this character was left unpolarized.

Supra-auricular Fold (Character 56; Fig. 26, 27).—Frost (1992) defined the supra-auricular fold as a continuation of the dorsolateral fold that passes above the tympanum. In crotaphytids, a similar fold is present; however, it originates from the postauricular fold at a point roughly midway between the dorsal and ventral borders of the external auditory meatus. Without strong evidence to the contrary, I treat the crotaphytid fold as homologous with that described by Frost (1992) and therefore apply his standardized nomenclature. The condition of the supra-auricular fold, in which it originates midway between dorsal and ventral borders of the external auditory meatus, is present in many iguanian taxa

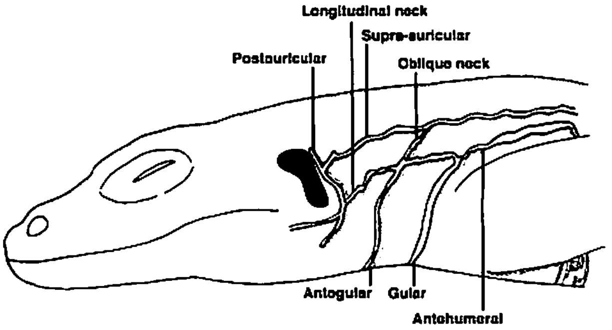

Fig. 27.—Lateral view of the neck folds of *Gambelia wislizenii* (SDSNH 68663). Fold terminology follows Frost (1992).

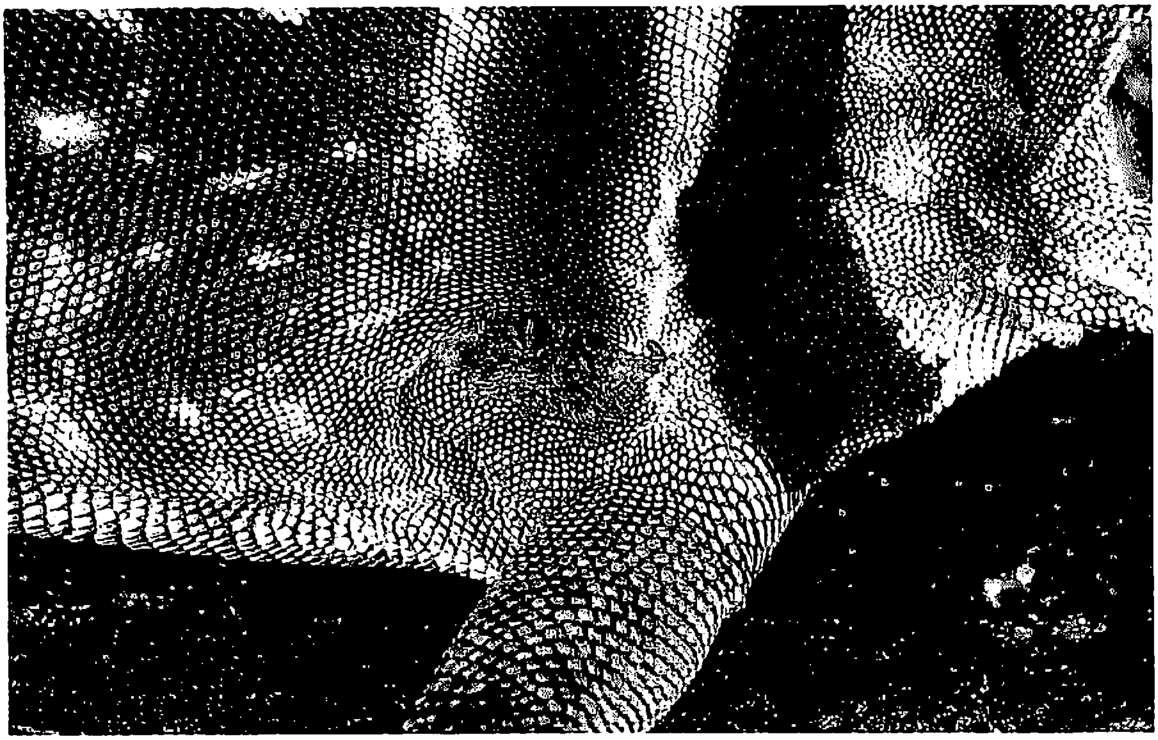

Fig. 28.—An antehumeral mite pocket in a juvenile *Crotaphytus grismeri*.

and, therefore, could not be included in the phylogenetic analysis.

The supra-auricular fold differs between *Crotaphytus* and *Gambelia*. In *Crotaphytus*, the fold extends posterodorsally at an angle of roughly 45 degrees. In *Gambelia*, the fold extends posteriorly along a horizontal plane. In most of the outgroup taxa that have a supra-auricular fold, the fold either projects posteriorly along a horizontal axis, or occasionally, posteroventrally. However, some taxa may have a *Crotaphytus*-like supra-auricular fold (often variably), including the phrynosomatids *Petrosaurus repens*, *Uta stansburiana*, *U. squamata*, *U. palmeri*, *Urosaurus auriculatus*, and *Phrynosoma coronatum*, the tropidurids *Leiocephalus schreibersi*, *L. melanochlorus*, and *L. psammodromus*, the hoplocercid *Enyalioides oshaughnessyi*, and the chamaeleonids *Uromastyx acanthinurus* and *U. philbyi*. Because of this variation and because many outgroup taxa cannot be scored for this feature, this character was left unpolarized.

Antehumeral Fold (Fig. 26–28).—The antehumeral fold of crotaphytids is strongly developed, curving posteriorly over the forelimb insertion. The deepest portion of the fold is directly dorsal to the forelimb, a condition rarely observed in the outgroups. Furthermore, the antehumeral fold often extends posteriorly beyond the forelimb insertion, then continues posteroventrally or ventrally forming a complete arc. This condition is again uncommon in the outgroups. However, there is sufficient variation within Iguania that I have chosen not to code this as a character. The antehumeral fold of *Crotaphytus dickersonae* is unique among crotaphytids in terminating anterior to the forelimb insertion. Although this condition is probably derived within Crotaphytidae, another character, presence or absence of an antehumeral mite pocket, is certainly not independent. Therefore, this character is considered under the section dealing with the antehumeral mite pocket.

Antehumeral Mite Pocket (Character 57; Fig. 28).—In all *Crotaphytus* except *C. dickersonae*, the antehumeral fold is well developed (deep), with an area of reduced squamation dorsal to the forelimb insertion. The pocket almost always is inhabited by large numbers of trombiculid mite larvae. The presence of a mite pocket in this portion of the ante-

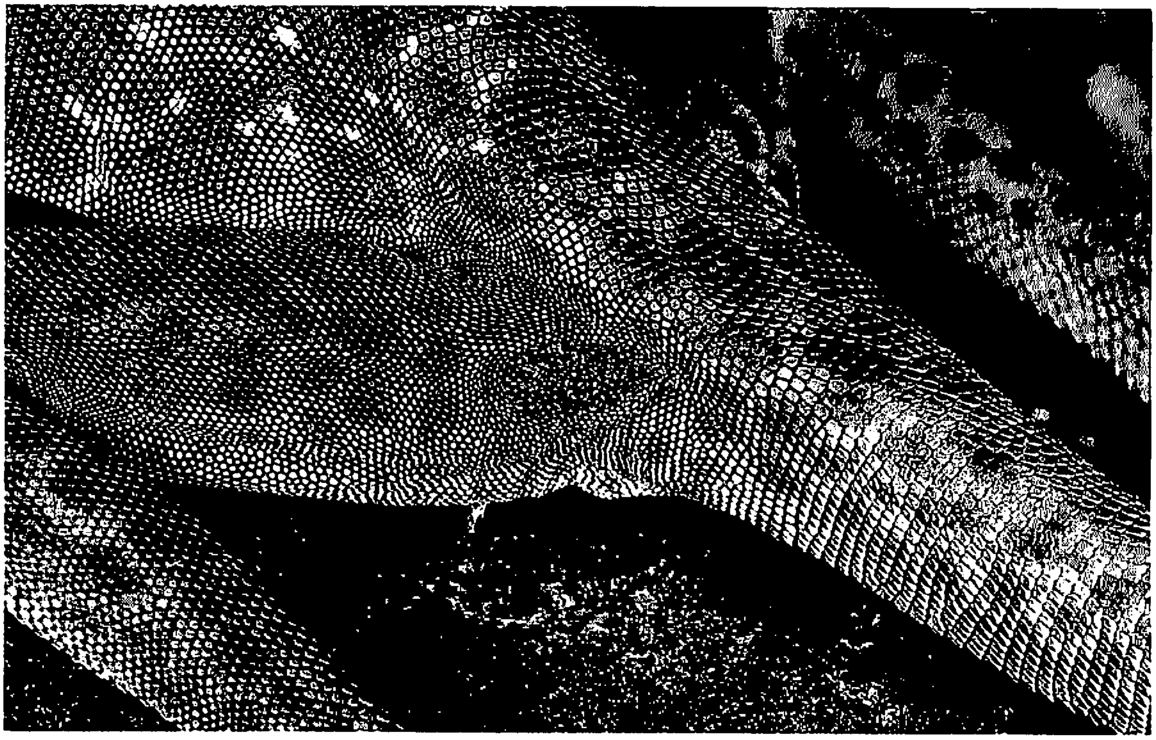

Fig. 29.—A postfemoral mite pocket in a juvenile *Crotaphytus bicinctores.*

humeral fold was not observed in any of the outgroup taxa examined and, thus, appears to be unique to *Crotaphytus,* excluding *C. dickersonae.* As discussed above, the antehumeral fold of *C. dickersonae* terminates further anteriorly than in any other crotaphytid, usually failing to reach the forelimb insertion, which probably explains the absence of an antehumeral mite pocket in this species.

Postfemoral Mite Pockets (Character 58; Fig. 29).—In most crotaphytids, subdermal mite pockets are present at the posterodorsal border of the hindlimb insertion where a patch of finely scaled or unscaled skin dips inward between M. iliofibularis and M. iliofemoralis. These pockets usually are inhabited by trombiculid mite larvae and occasionally ticks. Arnold (1986) noted that mite pockets, which may occur in a variety of anatomical regions, often vary both intra- and interspecifically in terms of their presence, degree of development (e.g., depth), and in the nature of their squamation, and in this respect Crotaphytidae is no exception. However, pockets were absent only in *Crotaphytus reticulatus* and occasionally in *C. collaris* and *C. nebrius.*

In *Crotaphytus,* the depth of the mite pocket may be correlated with the degree of development of the antehumeral mite fold. For example, in *C. reticulatus,* which lacks the postfemoral pocket, the mite pockets of the antehumeral fold (discussed above) are strongly developed. In contrast, the mite pockets of the antehumeral fold are absent in *C. dickersonae,* while the postfemoral pockets are the most strongly developed (deepest) of all *Crotaphytus.*

Postfemoral mite pockets are not unique to Crotaphytidae. Smith (1939) noted that they are present in seven species of *Sceloporus,* including the five species in his *S. variabilis* group, as well as *S. maculosus* and *S. gadoviae.* Shallow postfemoral pockets were also observed in *Uta squamata* and *U. palmeri,* but not other *Uta.* Although not observed here, shallow mite pockets are occasionally present in several species of *Urosaurus* (J. Wiens, personal communication, 1994). However, the absence of postfemoral pockets in *Phrynosoma,* the sand lizards, *Petrosaurus,* most *Uta* (in those species that lack pockets, mites may accumulate in the postfemoral region, but an obvious subdermal pocket is lacking), most *Urosaurus, Sator,* as well as most *Sceloporus,* suggests that the pockets observed in subsets of *Uro-*

saurus, Uta, and *Sceloporus* are not homologous with crotaphytid postfemoral pockets.

Most *Stenocercus* and at least two species formerly referred to *Ophryoessoides* (*S. ornatus* and *S. trachycephalus*) have postfemoral mite pockets (Fritts, 1974; Arnold, 1986). However, the postfemoral pocket of those *Stenocercus* species examined here (*S. trachycephalus, S. chrysopygus, S. guentheri, S. imitator, S. roseiventris*) occurs as a vertical fold along the lateral body wall immediately posterior to the hindlimb insertion and, thus, does not appear to be homologous with the postfemoral mite pocket of crotaphytids. Furthermore, postfemoral mite pockets appear to be absent from the basal lineages of Liolaeminae (*Phymaturus* and *Ctenoblepharys:* species examined include *Ctenoblepharys adspersus, Phymaturus* sp., *P. palluma, P. patagonicus, P. punae*), Leiocephalinae (G. Pregill, personal communication, 1993; verified in *Leiocephalus carinatus, L. inaguae, L. macropus, L. melanochlorus, L. pratensis* [folds present, but no reduction in squamation], *L. psammodromus, L. schreibersi*), and Tropidurini (*Uranoscodon superciliosus, Plesiomicrolophus koepkeorum, Microlophus theresioides, M. tigris, M. stolzmani,* personal observation). Thus, the postfemoral mite pockets of certain members of the Stenocercini are considered to be nonhomologous with crotaphytid postfemoral mite pockets.

Several oplurids have postfemoral mite pockets that appear to be structurally identical with those of crotaphytids. That is, the pocket occurs as an invagination between M. iliofibularis and M. iliofemoralis. Arnold (1986) noted the presence of postfemoral mite pockets in *Oplurus cuvieri* and *O. cyclurus* and I have observed them in *O. cyclurus,* as well as in *O. saxicola, O. fierinensis,* and *Chalaradon madagascariensis.* Postfemoral mite pockets appear to be absent in *O. quadrimaculatus.* Because we have no hypothesis of phylogenetic relationships for oplurids, it is not possible to say whether the pockets are derived within the family or were present ancestrally. Therefore, the possibility that postfemoral mite pockets were present in the common ancestor of Opluridae cannot be discounted.

Among iguanids, *Dipsosaurus dorsalis* has a weakly developed postfemoral pocket that occurs in the same anatomical position as the postfemoral mite pocket of crotaphytids. Because *Dipsosaurus* (along with the fossil species *Armandisaurus explorator*†) is the sister taxon of the remaining iguanids (de Queiroz, 1987; Norell and de Queiroz, 1991), the possibility that postfemoral pockets were present in the common ancestor of Iguanidae cannot be eliminated.

Postfemoral mite pockets appear to be absent from Corytophanidae, Hoplocercidae, Chamaeleonidae, and Polychrotidae, although all of their constituent species have not been examined. Although postfemoral mite pockets may have been present in the common ancestors of the families Opluridae and Iguanidae, their presence is most parsimoniously treated as the derived state for Crotaphytidae.

ADDITIONAL MORPHOLOGICAL CHARACTERS

Hemipenes (Character 59).—Hemipenes were examined for all of the crotaphytid species except *Crotaphytus reticulatus.* The hemipenes of crotaphytids are bulbous and weakly bilobed with a short median fissure separating the two lobes apically. The sulcus spermaticus is covered by a large fleshy flap of integument that folds over it from its lateral margin. This fold does not project directly toward the apex but rather extends laterally toward the outer margin of the lateral lobe. The sulcus spermaticus itself appears to terminate in a broad, shallow depression at the base of the lobes.

The entire sulcate surface of the hemipenis is only weakly ornamented with a fine papillate or dimpled texture. Immediately outside of the sulcus spermaticus, the surface is ornamented with plicae that are continuous with those of the asulcate surface. Distally, the lateral surfaces of the lobes bear small knob-like processes that are covered with extremely fine calyculae.

The base of the asulcate surface of the hemipenis is naked. More distally, ornamentation is present in the form of plicae and calyculae. The proximal lateral surfaces of the ornamented region of the hemipenis are covered by fine plicae. These plicae grade medially into calyculae and this calyculate zone extends distally toward the apex of the hemipenis where it spreads laterally. As a result, the entire surface of the hemipenis distal to the median apical fissure is ornamented with minute calyces. The lateral surface of each lobe bears a shallow depression ornamented with extremely fine calyces. The calyces reach their smallest sizes here and in the apical region of the hemipenis.

The only obvious difference between the hemipenes of *Crotaphytus* and those of *Gambelia* is in their relative size. The hemipenes of *Gambelia* are roughly twice the size of those of similar-sized *Crotaphytus.* Although the hemipenes of *Crotaphytus*

Fig. 30.—(A) *Gambelia wislizenii* (adult female), (B) *G. copei* (adult male), (C) *Crotaphytus reticulatus* (adult male), (D) *C. antiquus* (adult male).

appear to be unusually small, no attempt was made to polarize this character because adequate comparative material was not available.

Sexual Dimorphism (Character 60).—Most iguanian lizards are sexually dimorphic with males reaching larger SVLs than females (Fitch, 1981). This condition is exhibited in all *Crotaphytus* (Burt, 1929; Axtell, 1972; Fitch, 1981; McGuire, 1994; personal observation) as well as *Gambelia silus* (Tollestrup, 1979, 1982), while females are much larger than males in *G. wislizenii* (Tollestrup, 1979, 1982) and *G. copei* (Banta and Tanner, 1968). Sexual dimorphism in which males are larger than females appears to be the ancestral state for the families Chamaeleonidae (Parcher, 1974; Fitch, 1981), Iguanidae (Fitch, 1981; Gibbons, 1981; Carothers, 1984), Opluridae (Blanc and Carpenter, 1969), Phrynosomatidae (Fitch, 1981), and Tropiduridae (Dixon and Wright, 1975; Fitch, 1981; Cadle, 1991; Etheridge, 1992, 1994, 1995; Pregill, 1992; R. Etheridge, personal communication, 1994). The ancestral state is equivocal for Hoplocercidae (Duellman, 1978), Corytophanidae (Fitch, 1981), and Polychrotidae (Lazell, 1969; Fitch, 1981; Frost and Etheridge, 1989; Etheridge and Williams, 1991; Schwartz and Henderson, 1991). Although the data regarding sexual dimorphism in iguanians are somewhat fragmentary, the most parsimonious conclusion at this time is that the ancestral condition for Crotaphytidae is males larger than females. Therefore the character state present in *Gambelia copei* and *G. wislizenii* (females larger than males) is treated as the derived state.

COLORATION

Gravid and Subadult Coloration (Characters 61, 62; Fig. 31C, D).—All female crotaphytids display red or orange dorsal banding or spotting when gravid. Although Frost and Etheridge (1989) suggested that gravid coloration may be a synapomorphy for the family, the presence of gravid coloration in many phrynosomatids and tropidurids and several chamaeleonids (Cooper and Greenberg, 1992; personal observation) suggests that this condition may represent a synapomorphy for a more inclusive group than Crotaphytidae.

Subadult male *Crotaphytus collaris* develop a color pattern of red or orange dorsal banding that is very similar to that of gravid females, both in terms of its anatomical position and chromatic qualities of the pigments (Rand, 1986). The author has also observed this coloration in *C. bicinctores, C. dickersonae, C. grismeri, C. insularis, C. nebrius, C. reticulatus,* and *C. vestigium.* Rand (1986) demonstrated that the subadult male coloration of *C. collaris* is not induced by progesterone, as it is in females, which suggests that subadult male and gravid female coloration are independent. The presence in subadult males (but not subadult females) of orange or red banding similar to that of gravid females appears to be unique to *Crotaphytus.* The only species (that I am aware of) that exhibits a similar subadult coloration is *Microlophus delanonis* (Werner, 1978). This species has gravid coloration and juveniles of both sexes develop coloration similar to that of gravid females. Therefore, the presence of ephemeral red banding in subadult males is treated as the derived state.

Juvenile *Gambelia* are characterized by the presence of paravertebrally arranged rows of blood-red spots that extend from the top of the head to the proximal portion of the tail and may be present on the limbs as well. Each row generally consists of four large spots, although smaller spots may be present further laterally. These blood-red spots gradually fade into solid brown spotting in adult *Gambelia.* This condition, which was not observed in the outgroups, is coded as a character independent of the subadult male coloration character described for *Crotaphytus* because it does not occur in the same anatomical position and because it occurs in both sexes.

Tail Color (Characters 63–65; Fig. 31B, 31C, 32A–D; observable only in live individuals).—Adult *Crotaphytus dickersonae* females exhibit a unique feature among crotaphytids in that the hindlimbs and in particular the tail may be bright lemon yellow in comparison to other species in which the tail is the same general color as the rest of the body. This description is based on a sample of only two living females. An examination of preserved specimens suggests that many adult female *C. dickersonae* have a substantial blue component to their color pattern and, thus, the yellow pigmentation may be restricted to a particular season or age class. Because this type of yellow pigmentation in adult females was not observed in the outgroups, I consider it the derived state. However, bright coloration often fades in preservative and it is possible that this character state has been overlooked in other taxa.

Gambelia silus juveniles have yellow pigmentation in the form of a narrow strip along the posterior surface of the thigh and on the anteroventral surface of the tail. The pigmentation ends abruptly at the cloaca. Similar coloration was present in the only subadult female *C. antiquus* that was observed and this taxon is tentatively coded as having the same character state as that observed in *G. silus*. In other crotaphytids, the coloration of the tail and hindlimbs does not differ from that of the rest of the body. The presence of this juvenile coloration is treated as the derived state.

In those species with strongly laterally compressed tails (*C. bicinctores, C. dickersonae, C. grismeri, C. insularis*, and *C. vestigium*), a pale white or cream stripe runs down the dorsal surface of the tail (Fig. 31B, 32A–D). Presumably, the laterally compressed tail serves a display function and this white pattern may somehow enhance this role. The presence of a pale dorsal caudal stripe appears to be unique to these lizards as it was not observed in any of the outgroup taxa and is therefore considered to be the derived state.

Reticulate Pattern (Characters 66, 67; Fig. 30C, 30D, 31A–D, 32A–D, 33–35).—All male *Crotaphytus*, except some *C. nebrius*, have some form of white reticulation in the dorsal and/or gular pattern. Indeed, all *Crotaphytus* neonates have an extensive reticulated dorsal pattern, with some of the reticulations surrounding black pigment. This is a condition very similar to that seen in adult *C. reticulatus* and *C. antiquus* of both sexes. The extent and placement of the reticulated pattern varies considerably between species resulting in somewhat bewildering interspecific variation. Nevertheless, a pair of discrete characters were obtained from this aspect of the color pattern.

The first character (66) describes the presence or absence of a reticulate pattern in neonates. This condition is present in all *Crotaphytus* neonates, and is absent from *Gambelia* and the outgroups (although the number of outgroup species for which juveniles were examined is relatively small). Therefore, the presence of a neonatal pattern of white reticulations enclosing dark pigments is treated as the derived state.

A second character (67) is the presence of small, almost granular, reticulations on the ventrolateral surface of the abdomen. This condition is present only in *C. bicinctores* and *C. antiquus*, although the abdominal reticulations of *C. antiquus* are slightly larger than those of *C. bicinctores*. Ventrolateral abdominal reticulations were not observed in the outgroup taxa; therefore, their presence is treated as the derived state.

In *Crotaphytus*, there are two common dorsal pattern types, reticulation and spotting. It seems likely that spots are formed when reticulations have become fragmented. For example, in large *C. vestigium*, the typical reticulated pattern of the hindlimbs may be fragmented on the dorsal portion of the femoral region, resulting in spots. The anterior and posterior surfaces of the leg retain their reticulated pattern. Thus, the spotted pattern that occurs on the dorsum of all *Crotaphytus* except *C. reticulatus* and *C. antiquus* may be the derived condition. This same situation applies to additional characters associated with reticulation. However, the dangers of polarizing characters using ontogenetic methods are well known (de Queiroz, 1985; Mabee, 1989, 1993) and I present this scenario as a hypothesis and nothing more. The reticulated versus spotted adult dorsal body patterns are considered in the discussion of the white component of the dorsal pattern (see below).

White Component of Dorsal Pattern (Character 68; Fig. 30–32).—The white component of the dorsal pattern of crotaphytids is quite variable between species, but within species there is little variation. The two main dorsal pattern types present in adult *Crotaphytus* are reticulated and spotted. *Crotaphytus antiquus* and *C. reticulatus* exhibit the reticulated pattern, while the remaining species of *Crotaphytus* have a pattern that incorporates white spots or dashes. *Crotaphytus vestigium* and *C. insularis* (see below) each differ from the other spotted species in their own way. *Crotaphytus vestigium* has thin, white, transverse dorsal bands (Fig. 32C). Axtell (1972) noted the presence of similar banding in *C. bicinctores* from the northern portion of its range, which he attributed to the retention of the juvenile pattern. However, an examination of approximately 300 specimens of *C. bicinctores* in the California Academy of Sciences collection revealed that the white bands present in juveniles change during ontogeny into the broad, pale orange bands characteristic of adults. In adults that are dark from preservative, these orange bands fade and sometimes appear to be broad white bands. Although females may occasionally retain the juvenile white bands until near adult size is attained, males do not and no adult *C. bicinctores* that were not dark from preservative had white transverse banding. Only *C. insularis* approaches the condition of *C. vestigium*, with most specimens having broad, wavy dorsal lines or dashes and a few specimens having what appear to be wavy transverse dorsal bands (Fig. 32D). Although the wavy dashes present in *C. insularis* may be modified transverse dorsal bands, the *C. insularis* condition is treated as a separate character state and no *a priori* assumptions were made regarding the order of transformation. Because *Crotaphytus* and *Gambelia* are

Fig. 31.—(A) *Crotaphytus nebrius* (adult male), (B) *C. dickersonae* (adult male), (C) *C. dickersonae* (gravid female with gravid coloration), (D) *C. vestigium* (subadult male with orange subadult male coloration).

Fig. 32.—(A) *Crotaphytus bicinctores* (adult male), (B) *C. grismeri* (adult male), (C) *C. vestigium* (adult male), (D) *C. insularis* (adult male).

variable with respect to the white component of the dorsum, this variation was coded as an unordered multistate character. The *Gambelia* condition often consists of broad, white or cream-colored, offsetting transverse bars with large, brown dorsal spots and is coded as state 0; the *C. reticulatus* and *C. antiquus* condition of a white reticulum, some or all of which enclose black pigmentation, is coded as state 1; the pattern composed of numerous small white spots (present in *C. bicinctores, C. collaris, C. dickersonae, C. grismeri,* and *C. nebrius*) is coded as state 2; the *C. vestigium* condition of white, transverse dorsal bands on a background of white spots and dashes is coded as state 3, and the *C. insularis* condition of wavy, white dorsal dashes is coded as state 4. This character was left unpolarized.

Sexual Dichromatism (Character 69; Fig. 31B, C).—Sexual dichromatism is widespread within the Iguania (Cooper and Greenberg, 1992) and, thus, it is not surprising that most crotaphytids also display strong sexual dichromatism. However, *Gambelia* and *Crotaphytus reticulatus* generally lack sexual dichromatism in their permanent dorsal patterns (although *G. silus* and *C. reticulatus* do have male breeding coloration). There is obvious sexual dichromatism in the gular pattern and femoral pore coloration and a small amount of sexual variation in the collar of *C. reticulatus.* However, the remaining species of *Crotaphytus* have much more obvious sexual dichromatism throughout the year, with males differing from females in most aspects of dorsal coloration (e.g., much more vibrant blue, green, and/or yellow dorsal coloration in *C. collaris*), as well as in the gular pattern. Although sexual-dichromatism is present in many iguanian taxa, data could not be obtained for many of the more obscure and poorly known species. Therefore, this character was left unpolarized.

Paired Melanic Keels on Scales of Ventral Caudal Extremity (Character 70).—All *Crotaphytus* species except *C. reticulatus* (50 specimens examined) and *C. insularis* (23 specimens examined) are characterized by the presence, in at least some individuals, of darkly pigmented obtuse keels on the scales of the ventral surface of the tail tip (noted as present in *C. nebrius* and some *C. collaris* by Axtell and Montanucci, 1977). These take the appearance of paired dark spots that may extend along the ventral surface of the tail over the distal 2–30 mm. This feature is fixed in some species, polymorphic in others, and the percentage of individuals with the pigmented keels may vary extensively between populations of the same species.

Crotaphytus collaris is polymorphic with respect to this character and there is much geographic variation in the percentage of individuals with the paired pigmented scales. Individuals from regions of Mexico generally referred to the subspecies *C. c. fuscus* and *C. c. baileyi* usually possess this character (21 of 33 specimens examined). It is less often present (six of 23) in specimens from midwestern and southern United States (generally referred to the subspecies *C. c. collaris*). It was absent in all specimens of *C. collaris* examined from Arizona, eastern Utah, and western Colorado (generally referred to the subspecies *C. c. baileyi* and *C. c. auriceps*, $n = 38$). Although the percentage of individuals with pigmented keels varies regionally, the observed frequency for *C. collaris* (29 of 94) was employed in the phylogenetic analysis.

In *Crotaphytus nebrius*, this characteristic appears to be nearly fixed. The pigmented scales were observed in 48 of 49 specimens examined. The only specimen that lacked the scales (KU 121460) was from the Tucson Mountains, an isolated range inhabited by what may be a distinct species. Unfortunately, this is one of only two preserved specimens available from the Tucson Mountains (the other specimen, SDSNH 15208, had pigmented scales). The pigmented scales are much darker, and thus more obvious, in *C. nebrius* than in *C. collaris.*

Crotaphytus bicinctores is another species in which this characteristic is polymorphic. It was present in 37 of 79 specimens examined. However, the percentage of individuals with the pigmented scales varied considerably between populations. Specimens from southern populations (Palo Verde Mountains, California; Chocolate Mountains, California; Kofa Mountains, Arizona; Sentinel, Arizona) have the scales in high frequency (26 of 32), while specimens from more northern populations (Idaho; Inyo County, California; Washington County, Utah) usually lack them (present in three of 30 specimens examined).

The pigmented scales appear to be fixed in *Crotaphytus dickersonae* (present in 44 of 44 specimens examined), *C. grismeri* (present in ten of ten specimens examined), *C. vestigium* (present in 43 of 43 specimens examined), and in *C. antiquus* (present in 17 of 17 specimens examined). The presence of paired melanic keels on the distal caudal extremity is considered to be the derived state as they appear to be unique to *Crotaphytus.*

Black Oral Mucosa (Character 71).—In all crotaphytids except *Crotaphytus bicinctores, C. grismeri, C. insularis,* and *C. vestigium,* black pigments

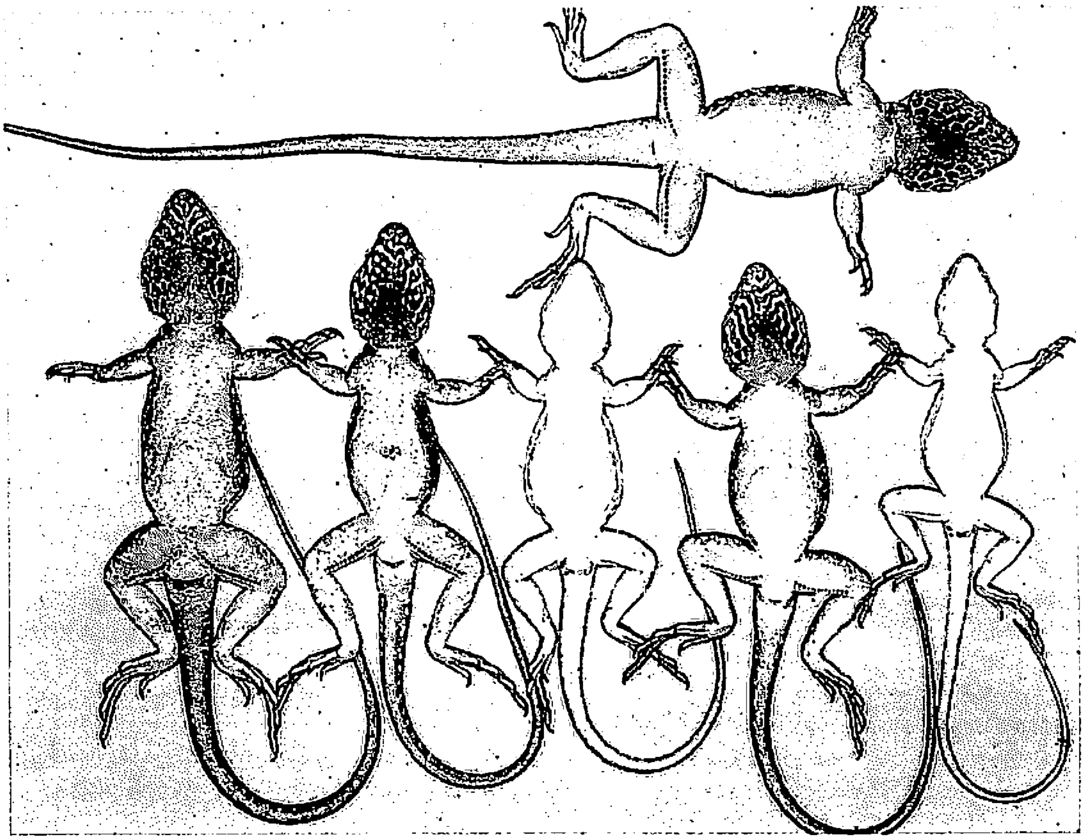

Fig. 33.—Ventral view of a series of *Crotaphytus collaris.*

are deposited in the oral mucosa and at least some of the underlying fascia of the M. adductor mandibulae complex. There is interspecific variation in the extent of the pigmentation as well. In *Gambelia, C. collaris, C. nebrius,* and *C. reticulatus,* the coverage and density of the oral melanin is extensive. The pigments are present on the floor of the buccal cavity as well as on the fauces of the roof of the cavity. In *C. antiquus* and *C. dickersonae,* black oral melanin is present but it is less extensive in both coverage and density. Stebbins (1954) noted that *G. wislizenii* from the Painted Desert region of Arizona may lack this coloration. However, this observation has not been confirmed in the present study and Stebbins himself (personal communication, 1991) does not recall where he obtained this information.

A black oral mucosa appears to be absent from all basal outgroup taxa outside of the family Polychrotidae (the throat lining is deep violet in *Tropidurus umbra,* Etheridge, 1970). Within Polychrotidae, black oral melanin is present in some *Polychrus* (*P. marmoratus, P. acutirostris*), *Pristidactylus volcanensis, Leiosaurus catamarcensis, Urostrophus vautieri* (Etheridge and Williams, 1991), *Anisolepis grilli* (Etheridge and Williams, 1991), *Phenacosaurus heterodermis,* and all three species of *Chamaeleolis* (Schwartz and Henderson, 1991). It is variably present in *Pristidactylus torquatus.* The absence of black oral melanin has been verified in *Polychrus liogaster, P. guttarosus, Pristidactylus achalensis, P. scapulatus, P. casuhatiensis, Leiosaurus belli, U. gallardoi, Enyalius bilineatus, E. brazilienesis, E. catenatus, E. iheringii, E. perditus,* and *E. pictus.* Although black oral melanin may prove to be the ancestral condition for Polychrotidae, the family does not appear to be the sister taxon of Crotaphytidae (Frost and Etheridge, 1989). Therefore, the presence of black oral melanin is treated as the derived state.

Collars (Characters 72–75; Fig. 30–36).—Although all *Crotaphytus* species are characterized by the presence of at least one collar, there is considerable interspecific variation. Most species have two well-developed black collars, with relatively thick white borders that encircle or partially encircle them. The collar configurations of *Crotaphytus reticulatus* and *C. antiquus* suggest that the transversely arranged series of black spots (each of which is bordered with white) present in these species may have

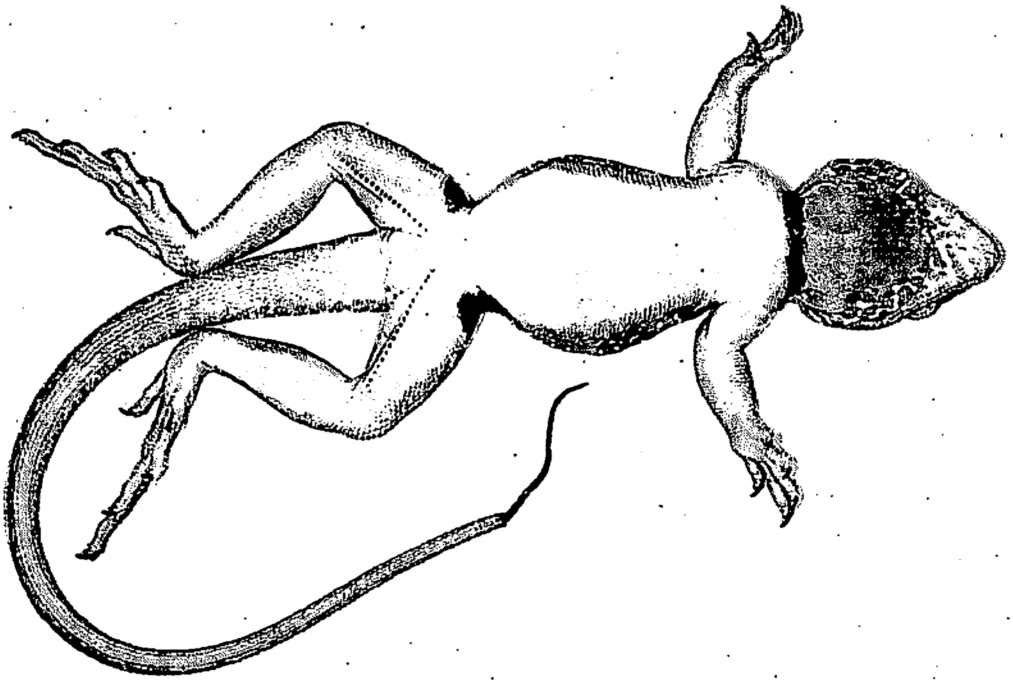

Fig. 34.—Ventral view of an adult male *Crotaphytus nebrius*.

been the precursor to the black collars outlined in white that are found in all *Crotaphytus* species. This is especially evident in the posterior collar markings, which in *C. reticulatus* are usually little more than a few closely approximating black spots with white borders. Furthermore, in most individuals there are dark pigments bleeding into the intervening areas between the black spots. A similar situation is sometimes present in the anterior collar as well. With respect to the outgroup taxa, it is unlikely that a white-bordered collar or pair of collars is the ancestral state in all but Opluridae (collars present in *O. cuvieri* and *O. cyclurus*). Therefore, the presence of white-bordered collars is treated as the derived state.

Additional variation occurs in *C. bicinctores*, *C. antiquus*, *C. collaris*, *C. dickersonae*, *C. grismeri*, and *C. nebrius*, where the posterior collars are either in contact or only narrowly separated at their medial margins (Fig. 30–32, 36). In *C. insularis* and *C. vestigium*, the posterior collars are broadly separated (Fig. 32C, D). The condition in *C. reticulatus* is more difficult to interpret because of the weak development of the posterior collar and it is tentatively coded as widely separated. Because *Gambelia*, the nearest outgroup to *Crotaphytus*, lacks collars, this character was left unpolarized.

In all adult male *Crotaphytus* except *C. collaris*, the anterior collar is complete ventrally by way of dark brown or black pigmentation within the transverse gular fold (Fig. 33–35). Because the nearest outgroup taxa lack collars, this character was left unpolarized.

In *Crotaphytus collaris* and *C. nebrius*, the posterior collar passes through the antehumeral fold before reaching the proximal dorsal surface of the brachium. A less developed condition usually occurs in *C. reticulatus*, where the collar passes through the extensive antehumeral mite pocket and isolated black patches may extend a short distance onto the proximal dorsal surface of the brachium. In *C. antiquus*, the posterior collar marking of males either terminates at the forelimb insertion or melanic spots extend onto the brachium, while in females, the collar marking generally terminates before entering the antehumeral fold (although in one individual [MZFC 6755], the marking seems to continue through much of the underlying mite pocket). In *C. dickersonae*, the posterior collar just reaches the dorsal surface of the forelimb insertion and may extend slightly onto the brachium as in *C. reticulatus*. However, the collar marking does not pass through the antehumeral fold in this species because the antehumeral fold terminates anterior to the posterior

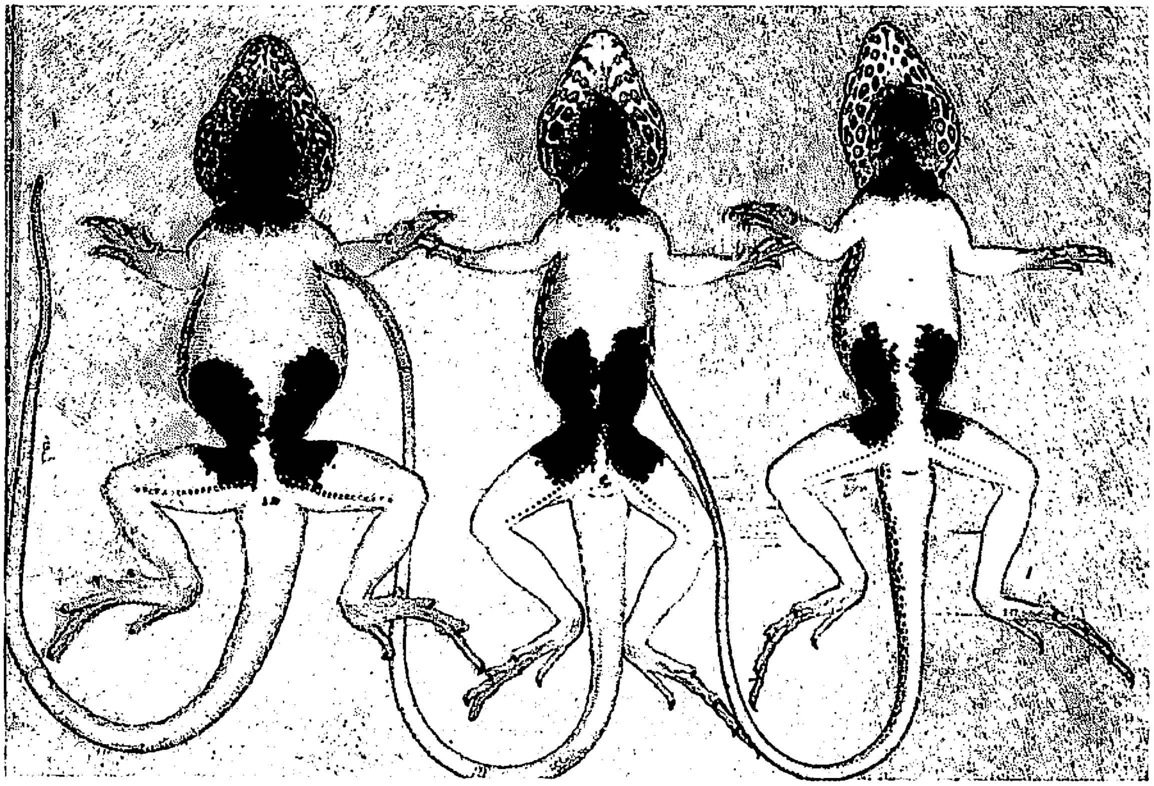

Fig. 35.—Ventral view of a series of adult male *Crotaphytus vestigium*.

collar. In *C. bicinctores* and *C. grismeri*, the posterior collar terminates within the antehumeral fold. In *C. vestigium* and *C. insularis*, the posterior collar almost always terminates before reaching the antehumeral fold. The extreme situation exists in *C. insularis* where, in the few individuals that have a posterior collar, it terminates just before reaching the antehumeral fold. This character is less consistent in females, especially with respect to *C. reticulatus*, in which females either lack collars or have them poorly developed. The four conditions described above were coded as separate character states of an unordered multistate character (state 0 = collar extends well out onto dorsal surface of brachium, state 1 = collar just reaches forelimb insertion, state 2 = collar terminates within antehumeral fold, state 3 = collar terminates before entering antehumeral fold). Again, because the nearest outgroups lack collars, this character was left unpolarized.

As stated above, all *Crotaphytus* species are characterized by the presence of at least one collar (but see *C. insularis* below). In fact, with few exceptions, all *Crotaphytus* species except *C. insularis* and female *C. reticulatus* have two collars. *Crotaphytus insularis* almost always have only the anterior collar, the posterior collar having apparently been lost (Fig. 32D). The fact that five specimens (CAS 21948, 50879, 86754, 148652; SDSNH 53064) have an extremely reduced, but visible, posterior collar is consistent with the hypothesis that collar reduction has occurred in this species. Males have a more densely pigmented anterior collar than females, which sometimes have no collar at all. This reduction in both the posterior and anterior collars appears to be derived and hence an autapomorphy for this insular species. In *C. reticulatus* females, the anterior collar marking may be lacking while the posterior collars remain. However, the posterior collar marking in both sexes of this species is often little more than a slightly modified band of black-filled reticulations. This variation was not included in the phylogenetic analysis because of the potential problem of lack of independence between this state and the wide separation of the posterior collars described above.

Dark Nuchal Spots (Character 76; Fig. 36).—A pair of black or dark spots usually occurs between the dorsal extensions of the anterior collar markings in *Crotaphytus reticulatus* (39 of 51), *C. antiquus* (16 of 16), and *C. collaris* (58 of 75), and are occasionally present in *C. nebrius* (12 of 51). The spots, which occur between the dorsal extensions of the anterior collar markings, appear to be homologous with the first transversely arranged row of black-filled hexagonal reticulations seen in *C. reticulatus*. In *C. antiquus*, the nuchal spots are always present, but often incompletely separated from the remainder of the anterior collar markings. Black nuchal spots are not present in the outgroup taxa and their presence is coded as the derived state.

Inguinal Patches (Characters 77, 78; Fig. 32C, 34, 35).—In several species of *Crotaphytus*, adult males develop dark brown or black ventral patches in the inguinal region. These patches vary considerably in size with *C. bicinctores, C. dickersonae, C. grismeri, C. insularis*, and *C. vestigium* having large patches and *C. antiquus, C. nebrius*, and *C. collaris* having smaller ones. All adult male *C. bicinctores, C. antiquus, C. dickersonae, C. grismeri, C. insularis, C. nebrius*, and *C. vestigium* develop these patches while only some *C. collaris* have them. Interestingly, only *C. collaris* from the western periphery of its range (in the area usually referred to the subspecies *C. c. baileyi*) are known to have inguinal patches. Thus, there are at least two characters associated with inguinal patches: size of the patches and the frequency with which they occur. Homology of the patches seems likely. Both large and small patches begin development as small ventral spots near the hind limb insertion and the large patches differ only in that they continue to become larger (and probably grow faster). Inguinal patches of the type present in some *Crotaphytus* are extremely rare in the outgroup taxa. Similar markings are present in *Uma exsul* and *U. paraphygas* (de Queiroz, 1989; although they occur more laterally than in *Crotaphytus*), *Uta nolascensis, Uromastyx hardwickii* (concentrated on the thigh), and *Enyalius iheringii* (again, more laterally oriented). This character has been coded two ways: first, as a binary character with the absence of inguinal patches (of any size) as state 0 and the presence of patches as state 1; and secondly, as a separate binary character with the presence of small patches as state 0 and the presence of large patches as state 1. Taxa without inguinal patches were scored as unknown ("?") for this second character. Because the first character (77) considers the frequency in which patches are present, the second character (78) does not take frequency into consideration. For character 78, the presence of small patches in any frequency is assigned state 0 and the presence of large patches in any frequency is coded as state 1.

Femoral Pore Secretions (Character 79; Fig. 22, 23, 33–35).—The femoral pore secretions of male *Crotaphytus reticulatus* and *C. antiquus* are jet black. Unlike other *Crotaphytus* species, such as *C. nebrius*, which often have grayish secretions, the subcutaneous glands themselves are also jet black. This condition was not observed in other species of iguanian lizards and is treated as the derived state.

Gular Pattern (Characters 80–82; Fig. 33–35).—There is much variation in the gular pattern of male *Crotaphytus*, especially in the wide-ranging species *C. collaris*. However, the general arrangement of the gular colors is similar in all of the species. For example, each has a relatively uniformly colored central gular region that is surrounded by a peripheral reticulated or spotted pattern superficial to the mandibles. It is in the context of this general pattern that the following discussion of variation is based. Because the pattern and extent of the gular coloration is sexually dichromatic, the following discussion pertains only to adult male *Crotaphytus*.

Adult male *Crotaphytus bicinctores, C. antiquus, C. dickersonae, C. grismeri, C. insularis, C. reticulatus*, and *C. vestigium* (Fig. 35) have a patch of black pigment in the posteromedial portion of the gular region. This pigmentation corresponds with that portion of the gular pouch that is depressed by the second ceratobranchials of the hyoid apparatus, and thus presumably increases the visibility of the depressed gular pouch during aggressive display. The black patch is continuous with the black pigmentation of the gular fold and the ontogenetic development of the gular patch suggests that it may be an extension of the gular fold coloration. However, the presence of black pigmentation in the gular fold and in the posteromedial portion of the central gular region are treated as separate characters because the presence of black pigmentation in the gular fold is not always associated with a black central gular patch (e.g., *C. nebrius*). Because the outgroups do not have a gular pattern that is similar to *Crotaphytus*, outgroup analysis cannot be utilized to assess polarity. Therefore, this character was left unpolarized.

There is considerable variation in the peripheral gular pattern of *Crotaphytus* as well. In all *Crotaphytus* except *C. nebrius*, the peripheral gular pattern is composed of white reticulations on a dark field. In most *C. collaris*, the dark pigmentation within each subquadrate reticulation has a light center, which results in a pattern reminiscent of the dorsal pattern of a jaguar. A similar pattern is sometimes evident in other species, such as *C. bicinctores*. In

C. nebrius, at least three easily recognizable patterns occur. One of two available preserved specimens from the Tucson Mountains (SDSNH 15208), as well as a photographic record of a specimen from this locality, have a peripheral gular pattern that is is very similar to that of *C. collaris.* More specifically, the pattern is composed of white reticulations filled with dark pigment (in this case dark blue) with pale, light centers. This is in striking contrast to the peripheral gular pattern of other *C. nebrius.* A second pattern, which has been observed in individuals from the Gila and Mohawk mountains of Arizona and the volcanic mountains immediately adjacent to Mexican Highway 2, at least as far south and east as 30 mi west of Caborca, Sonora, Mexico, is composed of radiating, oblique, white and dark blue stripes. These localities represent the northwestern portion of the range of *C. nebrius.* The third pattern, which corresponds to the pattern that Axtell and Montanucci (1977) used in their diagnosis of the species, is composed of pale white spots on a light blue to slate blue field. This pattern is seen in individuals from the Silverbell Mountains, the Estrella Mountains, and from Why, Arizona, and in one of three specimens from the Tucson Mountains, as well as from 16 mi south of Nogales, the vicinities of Nacori Chico and Bacadehuachi, 30 mi west of Caborca, and Guaymas, Sonora, Mexico. The presence of the second and third peripheral pattern types from identical localities, 30 mi west of Caborca and in the Tucson Mountains, suggests that these patterns may occur polymorphically. A similar situation occurs 0.9 mi south of Why, Arizona, where one individual has the pattern of white spots on a pale blue field and a second has a pattern intermediate between the spotted pattern and the one composed of radiating blue and white stripes (SDSNH 68645–46). Therefore, a taxonomic decision based on the differences between the spotted and striped gular patterns would certainly be premature.

A binary character associated with this variation in peripheral gular pattern is recognized. One state is the presence of a reticulated pattern in the peripheral gular region, the other is the presence of a pattern of pale spots or of radiating obliquely oriented stripes extending outward from the edge of the central gular region. If future collecting shows that the spotted and obliquely striped patterns do not grade into one another, and thus represent phylogenetically useful variations in gular pattern, then this *a priori* assessment of homology will have to be reevaluated. Neither of the two character states that I have described above are present in the outgroup taxa and therefore this character is left unpolarized.

The gular pattern of *Gambelia* is very different from that of *Crotaphytus.* The pattern is composed of longitudinally arranged black streaks or spots that extend from the posterior gular region to the mandibular symphysis. This gular pattern is present in all age classes of *Gambelia* and in both sexes, which is in contrast to the *Crotaphytus* condition, in which only adult males have a fully developed gular pattern. A single character was formulated in which the alternative states are a fully developed gular pattern in all age classes and in both sexes or a gular pattern that is only fully developed in adult males. Variation in the outgroups prevented polarization of this character.

Enlarged Melanic Axillary Patches (Character 83).—Enlarged melanic axillary patches are variably present in *Crotaphytus bicinctores, C. collaris, C. insularis, C. nebrius,* and *C. vestigium.* They are absent from *C. antiquus, C. dickersonae, C. grismeri,* and *C. reticulatus,* although in *C. reticulatus* and *C. antiquus,* black-filled reticulations may occur in the same axillary position as the melanic spots seen in other *Crotaphytus.* Axillary patches are not a fixed feature in any *Crotaphytus* species. Within *C. collaris,* they are present only in western populations from Arizona (and potentially Utah). Among the outgroup taxa, axillary patches were observed only in *Uta, Uma exsul,* and *Leiocephalus macropus* (within *Leiocephalus,* axillary patches are variable within *L. macropus,* but present in male *L. lunatus,* and male and female *L. greenwayi;* G. Pregill, personal communication, 1994), and, therefore, the presence of axillary patches is treated as the derived condition.

Ventrolateral Coloration (Character 84; often unobservable in preserved specimens).—Conspicuous ventrolateral coloration is present in adult male *C. dickersonae, Crotaphytus insularis,* and *C. vestigium,* as well as some male *C. collaris* and *C. nebrius.* The coloration present in *C. insularis, C. nebrius,* and *C. vestigium* appears to be ephemeral in nature, appearing only in the breeding season, whereas the coloration in *C. collaris* and *C. dickersonae* appears to be an extension of the normal adult male dorsal coloration onto the ventrolateral abdominal region. If this observation holds true, then it would appear unlikely that the ventrolateral coloration observed within all of these species is homologous. However, a survey of the ventrolateral coloration over the entire activity season has not been completed for each species and an assessment of homology is not possible.

Breeding male *Crotaphytus insularis* are characterized by olive green ventrolateral coloration that contrasts strongly with their brown dorsal coloration. Coloration that is identical in appearance occurs in *C. vestigium* males from the northern part of their range (north of Bahia de San Luis Gonzaga, Baja California, Mexico). Between Bahia de San Luis Gonzaga and Bahia de Los Angeles (a distance of approximately 120 km), a shift in ventrolateral coloration from olive green to golden orange occurs. The golden orange coloration is present in *C. vestigium* at least from Bahia de Los Angeles southward. In *C. nebrius*, coloration similar to that observed in southern *C. vestigium* may be present. This coloration has been observed in specimens from the Mohawk Mountains (Yuma County, Arizona), the Tucson Mountains (Pima County, Arizona), and 66.6 mi W Sonoita along Mexican Highway 2, and suggests that orange ventrolateral breeding coloration is characteristic of the species. *Crotaphytus dickersonae* and some *C. collaris* (those with turquoise or green dorsal coloration) may have bluish ventrolateral coloration.

Ventrolateral coloration was coded as an unordered multistate character with the absence of ventrolateral coloration coded as state 0, the presence of olive green coloration coded as state 1, the presence of orange coloration coded as state 2, and the presence of bluish coloration as state 3. *Crotaphytus vestigium* is polymorphic for this feature with states 1 and 2 present; *C. nebrius* is assigned state 2; *C. dickersonae* is assigned state 3; and *C. collaris* is assigned states 0 and 3. All other *Crotaphytus* and *Gambelia* are assigned state 0. No attempt was made to polarize this character.

Dorsal Coloration (Character 85; Fig. 30–32; some character states are not observable in preserved specimens).—The dorsal coloration of adult male *Crotaphytus* is characterized by much interspecific variation. *Crotaphytus reticulatus* has a dorsal coloration of golden tan, while *C. nebrius* has a similar straw yellow coloration that lacks the golden hue of *C. reticulatus*. *Crotaphytus dickersonae* is unique among *Crotaphytus* in that its coloration ranges from aquamarine to cobalt blue. The coloration of this species is generally dissimilar to that of *C. collaris*, although the aquamarine phase of *C. dickersonae* is occasionally approached by *C. collaris*. *Crotaphytus bicinctores*, *C. antiquus*, *C. grismeri*, *C. insularis*, and *C. vestigium* have a brown dorsal coloration. *Crotaphytus collaris* is extremely variable geographically, with some populations characterized by a turquoise body pattern with a yellow head (eastern Arizona, eastern Utah, western Colorado, western New Mexico, as well as some Great Plains populations, for example Altus, Oklahoma, and Flint Hills, Kansas), others by a bright green coloration (many eastern populations), others by a pale to dark brown coloration (Chihuahuan Desert populations in southern New Mexico, western Texas, and Chihuahua, Mexico), and still others by a combination of olive green and/or gray (Coahuila, Durango, Zacatecas). Most populations of *Gambelia* are off-white to tan in coloration. However, *G. copei* may range from golden tan to dark brown. An unordered multistate character was coded with the off-white to tan coloration of most *Gambelia* represented by state 0, the golden tan of *C. reticulatus* by state 1, the straw yellow coloration of *C. nebrius* by state 2, the blue coloration of *C. dickersonae* and some *C. collaris* by state 3, a brown coloration by state 4, and green and/or gray coloration by state 5. *Crotaphytus collaris* is considered polymorphic with states 3, 4, and 5 present, as is *G. copei* with states 0 and 4. This character was not polarized.

BEHAVIORAL CHARACTERS

Saxicoly (Character 86).—*Gambelia* and *Crotaphytus reticulatus* generally occur in flatland desert habitats and have a generalized terrestrial lifestyle. Montanucci (1965, 1967, 1969, 1971) performed ecological investigations of *Gambelia silus*, *G. wislizenii*, and *C. reticulatus* and concluded that they are virtually ecological equivalents. Although each will utilize rocks as perching points when they are available, they often are found in areas quite removed from any rocky habitat. Also consistent with the assumption that the terrestrial lifestyles of *Gambelia* and *C. reticulatus* are homologous is the common utilization of "freeze behavior" in *G. wislizenii* (McCoy, 1967), *G. copei*, and *C. reticulatus*. Montanucci (1967) described a similar behavior in young *G. silus*, although he later suggested that this behavior is rare in this species (Montanucci, 1978). When disturbed, these species often take refuge beneath a nearby bush and remain motionless, apparently relying on crypsis to avoid detection. In many cases, the lizard can be approached within one or two meters without causing it to flee. In contrast with the terrestrial lifestyles of *Gambelia* and *C. reticulatus*, the remaining species of *Crotaphytus* are saxicolous such that they appear to be extremely

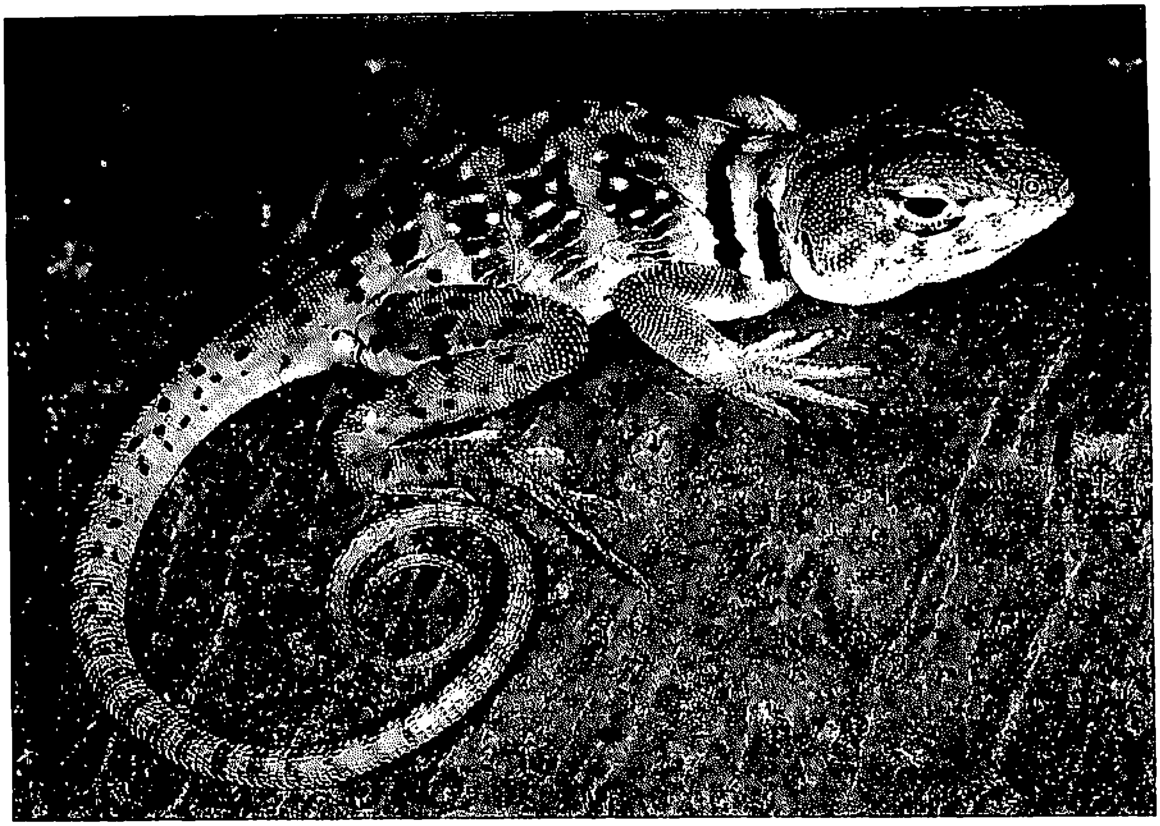

Fig. 36.—A juvenile *Crotaphytus nebrius* exhibiting lateral tail coiling behavior.

dependent on rocky habitats and are almost never observed in areas devoid of rocks. Montanucci (1974) noted that *C. collaris* may be found in arid flatland desert in at least two localities in Coahuila, Mexico. However, this behavior is certainly atypical for the species and similar behavior has not been observed by me or discussed in the literature for any of the other *Crotaphytus* taxa.

Although saxicoly certainly is not unique to *Crotaphytus,* this particular form of saxicoly, in which the lizards are restricted to boulder-strewn hillsides, alluvia, canyons, etc., where they scamper bipedally from rock to rock, perch atop rocks, and scan the immediate vicinity for potential prey and predators, is rare in the outgroup taxa. Nevertheless, because there are a diversity of character states present in the outgroup taxa that are absent from either *Crotaphytus* or *Gambelia* (such as arboreality, burrowing, and crevice-dwelling), a clear polarity decision was not possible for this character. Therefore, this character was left unpolarized.

Territoriality (Character 87).—Territoriality is known to be absent in *Gambelia wislizenii* (McCoy, 1967; Montanucci, 1970; Tanner and Krogh, 1974*a*; Tollestrup, 1979, 1982, 1983). *Crotaphytus* as well as *G. silus* are known to be highly territorial (Fitch, 1956; Montanucci, 1965, 1971; Yedlin and Ferguson, 1973; Moehn, 1976; Sanborn and Loomis, 1979; Tollestrup, 1979, 1982, 1983). It has not been determined whether territoriality is present or absent in *G. copei,* although the behavior of this species appears to be quite similar to that of *G. wislizenii.* Territoriality is widespread within Iguania, and is known to be present in all of the remaining iguanian families except Hoplocercidae (Carpenter, 1967; Stamps, 1977), a group for which data were unavailable. Of the many outgroup taxa that have been studied, Stamps (1977) could list only two, *Phrynosoma* and *Anolis agassizi,* that are known to lack territorial behavior. Therefore, the absence of territoriality is here treated as the derived state.

Lateral Tail Coiling (Character 89; Fig. 36).—All *Crotaphytus* coil their tails laterally when taking refuge under stones or debris, while at rest, and while hibernating (Legler and Fitch, 1957). Presumably, this behavior assists in keeping the tail out of the reach of predators. Lateral tail coiling is also known in the members of the *Anolis homolechis* complex of Cuba (Hardy, 1958; Ruibal and Williams, 1961) and in several species of *Leiocephalus* (C. A. Haas, S. B. Hedges, personal communication, 1994; K. de Queiroz, personal communication, 1995—although they are described as coiling their tails vertically over their backs by Schwartz and Henderson, 1991). However, these groups are nested within Polychrotidae and Tropiduridae, respectively, indicating that their behaviors are convergent with that observed in *Crotaphytus*. The presence of lateral tail coiling is considered to be the derived state.

Consumption of Vertebrates.—All crotaphytids except *Crotaphytus antiquus, C. grismeri,* and *C. nebrius* have either been documented in the literature to include vertebrates in their diets (*C. bicinctores*: Banta, 1960; Snyder, 1972; Nussbaum et al., 1983; *C. collaris*: Fitch, 1956; McAllister and Trauth, 1982; *C. reticulatus*: Klein, 1951; Montanucci, 1971; *Gambelia copei*: Banta and Tanner, 1968; Montanucci, 1965; *G. wislizenii*: Stejneger, 1893; McCoy, 1967; Montanucci, 1967; Snyder, 1972; Tanner and Krogh, 1974*a*; Parker and Pianka, 1976; Tollestrup, 1979, 1983; Pietruszka et al., 1981; Crowley and Pietruszka, 1983) or have been observed to do so by the author. The primary vertebrate prey is other lizards, although rodents and snakes also have been recorded. There appears to be variation in the relative proportion of vertebrates included in the diets of the various species, with *Gambelia wislizenii* (Parker and Pianka, 1976; Tollestrup, 1979, 1982, 1983) and *G. copei* consuming a greater proportion of vertebrate prey than other species.

Many other iguanian species are known to eat vertebrates, including the phrynosomatid genera *Petrosaurus, Uma, Holbrookia,* and *Sceloporus,* which are all known to include other lizards in their diets (Stebbins, 1985); the corytophanid *Basiliscus* (Van Devender, 1982); the polychrotid *Anolis equestris* (Ruibal, 1964); and the chamaeleonids *Chlamydosaurus kingii* and *Physignathus lesueurii* (Cogger, 1992). I have not attempted to review the feeding habits of all of the potential outgroup taxa, but it is likely that many other species have similar feeding habits. Thus, the presence or absence of carnivory may not be a polarizable character, limiting its usefulness in this analysis. Furthermore, since most lizards will eat anything palatable that they are able to overcome, the inclusion of vertebrates in the diet may be, at least in part, a function of maximum adult size. For these reasons, this characteristic was not included in this analysis. However, the carnivorous predatory habits of *Crotaphytus* and *Gambelia* are consistent with a hypothesis of crotaphytid monophyly.

Vocalization.—The ability to vocalize is rare in squamates, with gekkotans being the only family in which it is known to occur commonly. Within iguanian lizards, vocalization is apparently limited to crotaphytids and certain polychrotids. A squealing sound is known to be emitted by *Gambelia wislizenii* (Jorgenson et al., 1963; Wever et al., 1966; Smith, 1974) and *Crotaphytus bicinctores* (Smith, 1974) during periods of stress. Similar vocalizations were discussed by Ruibal (1964) in three species of Cuban anoles, *Anolis isolepis, A. lucius,* and *A. vermiculatus* and by Lynn and Grant (1940) in *A. grahami* and *A. opalinus* (also noted in *A. grahami* by Etheridge, 1955). Because vocalization data are lacking for the majority of crotaphytid species, I have not included this character in the phylogenetic analysis. However, as with carnivory, the presence of vocalization in some species of *Crotaphytus* and *Gambelia* is consistent with the hypothesis of crotaphytid monophyly.

CHARACTER LIST

The following character list includes the morphological characters (informative or uninformative) discussed in the text, as well as the nine informative allozyme characters (characters 89–98) that could be coded using the Manhattan distance frequency approach discussed in Wiens (1995). One multistate morphological character (31) was also coded using the Manhattan distance frequency approach. Its step matrix is presented in Appendix 4 along with the step matrices for the allozyme characters. Character descriptions followed by (P) are polarized, those followed by (U) are unpolarized, and those followed by (UO) are unordered. Characters 28, 68, 75, 84, and 85 were not analyzed using frequency coding (see Materials and Methods).

SKULL AND MANDIBLE

1. Nasal process of the premaxilla (P): (0) broad, (1) narrow and elongate.
2. Ventral suture between vomers and premaxilla (P): (0) does not form a strong vertical ridge, (1) forms a strong vertical ridge.
3. Nasals (P): (0) do not overlap nasal process of the premaxilla anterior to posterior extent of

external nares, (1) overlap nasal process of the premaxilla anterior to posterior extent of external nares.

4. Prefrontals (P): (0) not in contact with jugals, (1) contact jugals.
5. Cranium (U): (0) vaulted, (1) not vaulted.
6. Postorbitals (P): (0) weakly overlapped dorsally by frontal and parietal, (1) strongly overlapped dorsally by frontal and parietal.
7. Tubercle on anterolateral portion of postorbitals (P): (0) absent, (1) present.
8. Posterior border of parietal roof (P): (0) approximately twice as wide as narrowest portion of frontal bone (unconstricted), (1) equal in width or only slightly wider than narrowest portion of frontal bone (constricted).
9. Supratemporal processes (in lateral view) (P): (0) tapered, rapidly narrowing dorsoventrally at their midpoints; (1) not tapered, remain broad over entire length.
10. Supratemporals (P): (0) broadly exposed on the lateral surface of the supratemporal process of the parietal, (1) lies in a groove on ventral surface of supratemporal process of parietal.
11. Septomaxillae (P): (0) wide, (1) narrow.
12. Suture of maxillae with premaxilla (P): (0) not saddle-shaped, no process of the maxilla overlaps the lateral border of the premaxillary base; (1) saddle-shaped, a process of the maxilla overlaps lateral border of premaxillary base.
13. Shape of maxilla–palatine articulation (U): (0) low arch, (1) triangular.
14. Jugal–ectopterygoid tubercle (P): (0) absent, (1) present.
15. Angle of jugal along anteroventral border of orbit (P): (0) approximately 45 degrees, (1) approximately 90 degrees (box-like condition).
16. Extravomerine bones (P): (0) absent, (1) at least one present.
17. Palatine foramen (U): (0) present, (1) absent.
18. Transverse process of the pterygoid with (U): (0) weakly developed ventral process, (1) strongly developed ventral process.
19. Paraoccipital processes project posteriorly (P): (0) to level of occipital condyle, (1) well beyond occipital condyle.
20. Angle of the quadrate process of the pterygoid (U): (0) approximately 18 degrees, (1) approximately 26–31 degrees.
21. Posterior projection of ectopterygoid crest (U): (0) present, (1) absent.
22. Posterior projections of parabasisphenoid (P): (0) reach the sphenoccipital tubercles; (1) terminate at, or anterior to, the base of the sphenoccipital tubercles.
23. Anterior extent of angular (U): (0) never reaches the fourth dentary tooth (counting forward from the posteriormost tooth) and rarely extends anteriorly beyond the posteriormost tooth, (1) extends at least to the fourth tooth (counting forward from the posteriormost tooth) and usually beyond.
24. Posterior mylohyoid foramen (U): (0) equal with apex of coronoid, (1) posterior to apex of coronoid.
25. Posterolingual process of the coronoid (P): (0) oriented vertically, (1) angled posteroventrally at approximately 45 degrees.
26. Bony shelf extending between medial process of surangular and ramus of mandible (P): (0) absent, (1) present.
27. Lateral process of surangular (P): (0) absent or present as a weakly elevated ridge, (1) present as a large protuberance.
28. Ridge on lateral surface of surangular (P, UO): (0) absent, (1) moderately developed, (2) strongly developed such that the dorsal surface of the mandible is concave.
29. Tympanic crest (P): (0) forms lateral border of retroarticular process, (1) curves posteromedially.
30. Maxillary and dentary teeth (P): (0) stout, either straight or slightly recurved; (1) long, slender, and more strongly recurved.
31. Number of premaxillary teeth (U, UO): (0) five, (1) six, (2) seven, (3) eight, (4) nine.
32. Palatine teeth (P): (0) absent, (1) present.
33. Pterygoid tooth patch (P): (0) follows margin of interpterygoid vacuity, (1) curves posterolaterally.

HYOID APPARATUS

34. Ceratohyals (U): (0) without hook-like processes on proximal, medial edge; (1) with hook-like processes on proximal, medial edge.
35. Length of second ceratobranchials (U): (0) approximately one-half length of ceratohyals, (1) more than two-thirds length of ceratohyals.
36. Second ceratobranchials (P): (0) in contact medially, (1) widely separated.

MISCELLANEOUS FEATURES OF THE HEAD SKELETON

37. Skull rugosity at some point in ontogeny (U): (0) absent, (1) present.

POSTCRANIAL SKELETON

38. Zygosphenes (P): (0) not separated from prezygapophyses by notch, (1) separated from prezygapophyses by notch.
39. Tail shape (P): (0) round or subcylindrical without well-developed dorsal and ventral fat bodies, (1) laterally compressed with well-developed dorsal and ventral fat bodies.
40. Autotomic fracture planes of caudal vertebrae (P): (0) present, (1) absent.
41. Number of xiphisternal ribs (P): (0) two, (1) one.
42. Notch on the anterior edge of the suprascapular cartilage (P): (0) absent, (1) present.
43. Posterior coracoid fenestrae (P): (0) absent, (1) present.
44. Calcified cartilage anterior border of scapular fenestra (P): (0) present, (1) absent.
45. Clavicular fenestrations (P): (0) absent, (1) present.
46. Termini of iliac blades (U): (0) laterally compressed, (1) round.
47. Arch formed by contact of the medial and lateral plantar tubercles (P): (0) absent, (1) present.

SQUAMATION

48. Rostral scale (U): (0) broad, approximately four times wider than high; (1) narrow, approximately two times wider than high.
49. Some of the prefrontal, frontal, interparietal, and parietal scales are (U): (0) enlarged relative to the surrounding scales in such a way as to form conspicuous supraorbital semicircles, (1) not enlarged relative to surrounding scales such that conspicuous supraorbital semicircles are not distinguishable.
50. Elongate scale in subocular series (P): (0) present, (1) absent.
51. Terminal supradigital scales (P): (0) not elevated from dorsal surface of claws, (1) elevated from dorsal surface of claws.
52. Femoral pore series (P): (0) terminates before reaching inferior angle of knee, (1) extends beyond inferior angle of knee.
53. Femoral pores (P): (0) much larger and more strongly developed in males than females, (1) roughly equal in size or only slightly larger in males than females.
54. Distal tail skin (P): (0) bound to underlying musculature, (1) loosely adherent to underlying musculature.
55. Posteromedially angled folds within gular fold (U): (0) present, (1) absent.
56. Angle of supra-auricular fold (U): (0) horizontal, (1) at 45-degree angle.
57. Antehumeral mite pockets (P): (0) absent, (1) present.
58. Postfemoral mite pockets (P): (0) absent, (1) present.

ADDITIONAL STRUCTURAL CHARACTERS

59. Hemipenes (U): (0) large, (1) small.
60. Sexual dimorphism (P): (0) males larger than females, (1) females larger than males.

COLORATION

61. Ephemeral orange coloration in subadult males (P): (0) absent, (1) present.
62. Paired, paravertebrally arranged, blood-red spots in juveniles of both sexes (P): (0) absent, (1) present.
63. Bright yellow tail coloration in adult females (P): (0) absent, (1) present.
64. Bright yellow tail coloration in juveniles of both sexes (P): (0) absent, (1) present.
65. Off-white stripe on dorsal crest of tail (P): (0) absent, (1) present.
66. Juvenile dorsal pattern with a white reticular component (P): (0) absent, (1) present.
67. Granular reticulations on ventrolateral surface of abdomen (P): (0) absent, (1) present.
68. White component of adult dorsal body pattern in the form of (U, UO): (0) broad, offset, transverse bars; (1) a reticulum over the entire dorsal surface; (2) spots; (3) spots along with slender transverse dorsal stripes; (4) spots along with wavy lines and dashes.
69. Sexual dichromatism of the dorsal pattern (U): (0) absent; (1) present, such that the dorsal coloration of males and females is conspicuously different.
70. Paired melanic keels on ventral caudal extremity (P): (0) absent, (1) present.
71. Black oral melanin (P): (0) absent, (1) present.
72. Black collar or collars with white borders (P): (0) collars absent, (1) collars present.
73. Posterior collar markings (U): (0) in contact dorsally or nearly so, (1) widely separated dorsally.
74. Anterior collar (U): (0) incomplete ventrally (no dark pigments in gular fold), (1) complete ventrally (dark pigments present in gular fold).
75. Ventral extent of the posterior collar (U, UO): (0) extends onto dorsal surface of brachium, (1)

just reaches forelimb insertion, (2) terminates within antehumeral fold, (3) terminates before entering antehumeral fold.

76. Dark nuchal spots (P): (0) absent, (1) present.
77. Inguinal patches (P): (0) absent, (1) present.
78. Inguinal patches (U): (0) small, (1) large (taxa without inguinal patches coded as unknown ["?"])
79. Femoral pore secretions (P): (0) off-white to gray, (1) black.
80. Black pigmentation in central region of gular pattern (U): (0) absent, (1) present.
81. Peripheral gular pattern (U): (0) reticulated, (1) pale spots or radiating oblique stripes.
82. Gular pattern (U): (0) present only in adults and well developed in males only, (1) well developed in all age classes and in both sexes.
83. Enlarged melanic axillary patches (P): (0) absent, (1) present.
84. Ventrolateral coloration (P, UO): (0) does not differ from ventral coloration (white), (1) olive green, (2) orange, (3) blue.
85. Dorsal coloration (U, UO): (0) off-white to tan; (1) golden tan; (2) straw yellow; (3) aquamarine to cobalt blue; (4) brown; (5) olive green, turquoise, or gray.

BEHAVIOR

86. Saxicoly (including the use of saltatory bipedal locomotion in rocky habitats) (U): (0) absent, (1) present.
87. Territoriality (P): (0) present, (1) absent.
88. Lateral tail coiling (P): (0) absent, (1) present.

ALLOZYMES

89. H-LDH (U): four electromorphs.
90. aGPD (U): two electromorphs.
91. 6-PGD (U): three electromorphs.
92. ICDs (U): four electromorphs.
93. ICDm (U): four electromorphs.
94. GOTs (U): three electromorphs.
95. Pro (U): two electromorphs.
96. Est1 (U): three electromorphs.
97. Hbpf (U): two electromorphs.
98. Tr (U): four electromorphs.

RESULTS

An initial analysis was performed on the morphological data set of 88 characters (allozyme data of Montanucci et al. [1975] not included). This resulted in the discovery of a single tree (Fig. 37) with a length of 12,334 (123.34 when the effect of weighting the characters is removed) and a consistency index (CI; excluding uninformative characters) of 0.761, a retention index (RI) of 0.848, and a g_1 tree length frequency distribution skewness value of -1.49 (the critical g_1 value for this data set when randomized is -0.16 [$P \leq 0.01$]); Table 1). This CI is greater than that expected for an analysis of 13 taxa (expected CI = 0.649; Sanderson and Donoghue, 1989), indicating that there is less homoplasy than expected in these data when compared with the 60 data sets reexamined by Sanderson and Donoghue (1989). The g_1 value is strongly left skewed suggesting that the data are phylogenetically informative. The tree generated in the bootstrap analysis is presented in Figure 38.

Reanalysis of the allozyme data set of Montanucci et al. (1975) using the Manhattan distance frequency approach resulted in the discovery of a single most parsimonious tree (Fig. 39A). The tree length frequency distribution data, summarized by the g_1 statistic (Hillis and Huelsenbeck, 1992), suggests that there is phylogenetically informative signal in this data set (observed g_1 value of -0.50; the critical g_1 value for this data set when randomized is -0.45 [$P \leq 0.01$]). The bootstrap tree for the analysis is given in Figure 39B (see comments below regarding interpretation of bootstrap P values).

Because analysis of both the morphological and allozyme data sets suggests that they contain phylogenetic signal, these data sets were combined and the larger data set was analyzed. Analysis of the combined morphology and allozyme data sets resulted in the same tree as did the analysis of the morphology data alone (Fig. 37). The tree length is 139.91, while the CI (excluding uninformative characters) for the combined tree is 0.761, the RI is 0.848, and the g_1 value is -1.45 (critical g_1 value $= -0.15$ [$P \leq 0.01$]). PAUP is unable to incorporate the step matrix characters into the CI and RI calculations, which explains why the CI and RI values are identical to those discovered in the analysis of the morphological data alone. The g_1 and CI values indicate that the data harbor substantial phylogenetic signal. The 50 percent majority-rule consensus tree generated in the bootstrap analysis of the com-

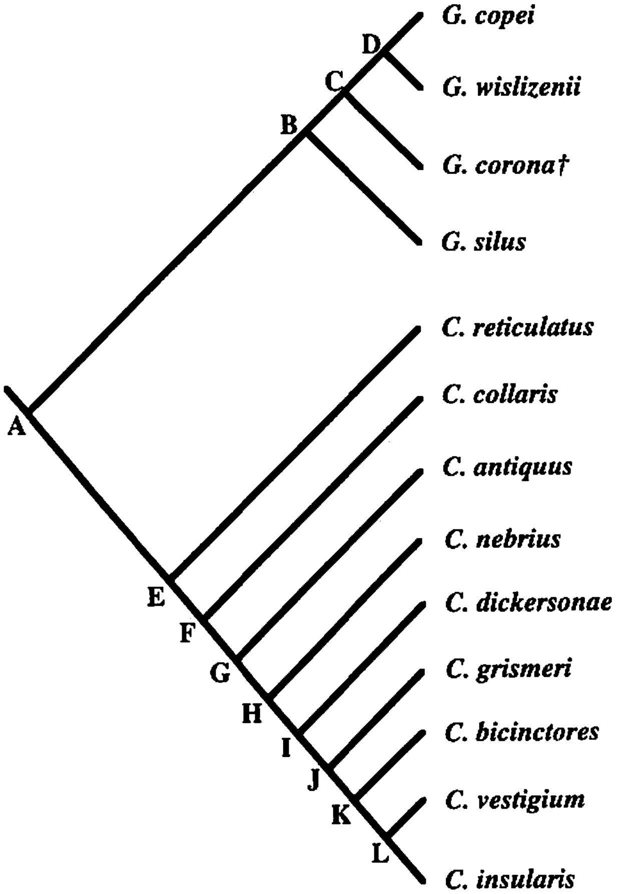

Fig. 37.—Cladogram discovered in the morphology-only and combined morphology + allozymes data analyses.

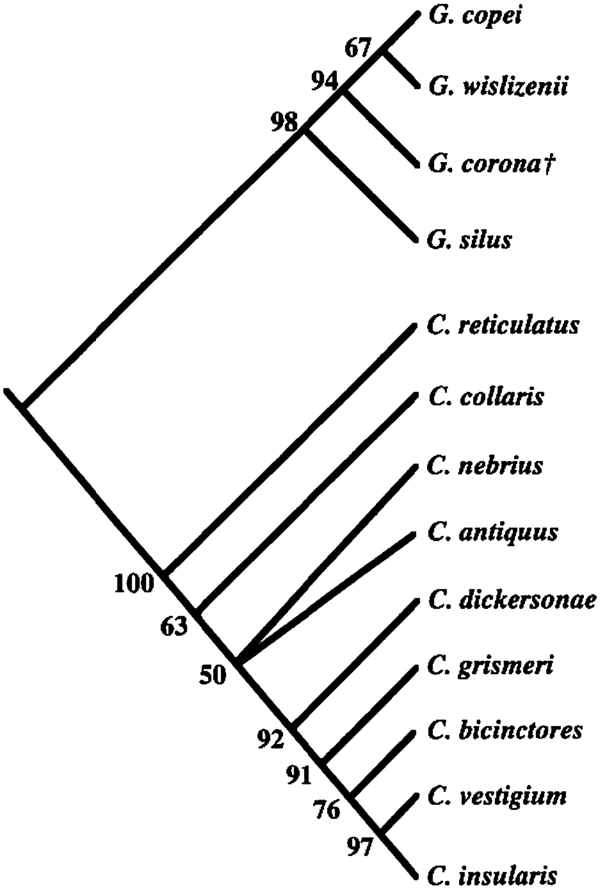

Fig. 38.—The 50 percent majority-rule consensus tree generated from the bootstrap analysis of the morphology-only data set.

bined data set is presented in Figure 40. The bootstrap analysis and g_1 values indicate that there is similar support for tree A with or without the allozyme data.

Reanalysis of the allozyme data set using the polymorphic coding and Mabee and Humphries (1993) approaches each resulted in different trees than that estimated using the step matrix approach. However, the combined analyses always resulted in the same tree as the morphology data alone, regardless of the coding approach employed with the allozyme data.

Character support for each stem of the cladogram discovered in the combined analysis (Fig. 37) is presented below. A complete listing of apomorphies, including the autapomorphies of the terminal taxa, is presented in Appendix 5. Transformations that are described as "unambiguous" are supported under both ACCTRAN and DELTRAN optimization. Therefore, when a node is described as "ambiguously" supported by a particular character state change, this means that the character in question supports this node under either ACCTRAN or DELTRAN optimization but not under both. "Fixed" transformations are those that involve a change from one fixed state to another (state "a" to state "y," or vice versa). When a transformation is not fixed it may be referred to as "polymorphic." Such transformations involve incomplete changes (for example from state "a" to state "m") and receive a reduced weight due to the frequency coding approach employed. Unambiguous fixed transformations include those character state changes from one fixed state to another that are discovered under both ACCTRAN and DELTRAN optimization.

Stem A (Crotaphytidae) is supported by 11 unambiguous transformations. Five of the synapomorphies represent fixed character state changes: 4.1 (prefrontals contact jugals), 6.1 (parietal and frontal strongly overlap the postorbital), 14.1 (jugal–ectopterygoid tubercle present), 29.1 (tympanic crest of the retroarticular process curves posteroventrally), and 71.1 (black oral melanin present, reversed in

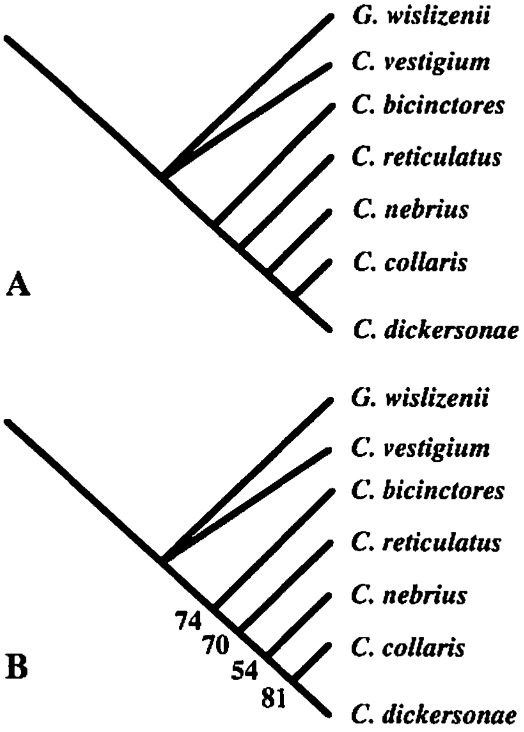

Fig. 39.—(A) The single most parsimonious tree discovered in the reanalysis of the allozyme data set of Montanucci et al. (1975) employing the approach in which frequency values are encoded into step matrices using Manhattan distances. (B) The 50 percent majority-rule consensus tree generated in the bootstrap analysis of this data set.

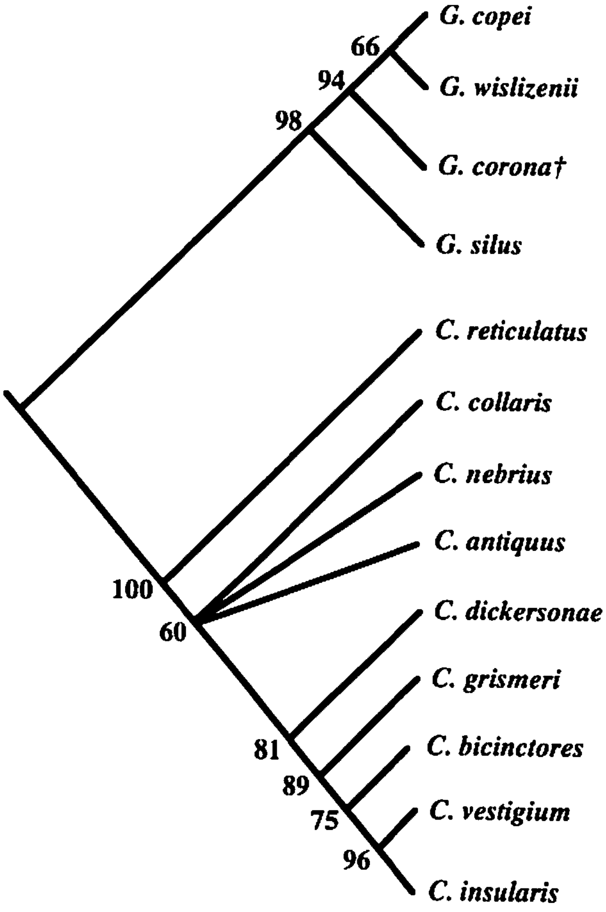

Fig. 40.—The 50 percent majority-rule consensus tree generated in the bootstrap analysis of the complete (morphology + allozymes) data set.

stem J). Six additional unambiguous yet polymorphic apomorphies support this stem: 10.1 (supratemporal lies in a groove in ventral surface of supratemporal process of parietal, 23/24 of one step under ACCTRAN optimization, 2/24 of one step under DELTRAN optimization), 26.1 (bony shelf extends between medial process of surangular and ramus of mandible, 2/24 of one step under both ACCTRAN and DELTRAN optimization), 32.1 (palatine teeth present, 16/24 of one step ACCTRAN, 13/24 of one step DELTRAN), 42.1 (scapular notch present, 10/24 of one step ACCTRAN, 5/24 of one step DELTRAN), 43.1 (posterior coracoid fenestrae present, fixed ACCTRAN, 16/24 of one step DELTRAN), and 45.1 (clavicular fenestrations present, fixed ACCTRAN, 8/24 of one step DELTRAN). Finally, Crotaphytidae may also be supported by two ambiguously placed synapomorphies: 40.1 (autotomic fracture planes of caudal vertebrae absent, 4/24 of one step ACCTRAN) and 58.1 (postfemoral mite pockets present, fixed ACCTRAN).

Stem B (*Gambelia*) is supported by 13 unambiguous synapomorphies, six of which represent fixed character state changes: 12.1 (saddle-shaped suture between premaxilla and maxilla), 30.1 (slender, recurved maxillary and dentary teeth), 44.1 (loss of the calcified cartilage border of the scapular fenestra), 46.1 (termini of the iliac blades round), 52.1 (femoral pore series extends beyond the inferior angle of the knee), and 62.1 (paired, paravertebrally arranged, blood-red spots present in juveniles of both sexes). This stem is also supported by seven unambiguous but polymorphic apomorphies: 2.1 (articulation between premaxilla and vomers in the form of a vertical ridge, 23/24 of one step ACCTRAN, fixed DELTRAN), 15.1 (angle of jugal along anteroventral border of orbit approximately 90 degrees, 12/24 of one step under both ACCTRAN and DELTRAN), 17.1 (palatine foramen absent, 19/24 of one step ACCTRAN, 18/24 of one step DELTRAN), 24.1 (posterior mylohyoid foramen posterior to apex of coronoid, 20/24 of one step under both ACCTRAN and DELTRAN), 26.1 (bony shelf between the median process and ramus of the mandible, 22/24 of one step under both ACCTRAN and DELTRAN), 36.1 (second ceratobranchials widely separated, fixed ACCTRAN, 16/24 of one step DELTRAN), and 41.1 (one rather than two xiphisternal ribs, 20/24 of one step under both ACCTRAN and DELTRAN). This stem also may be supported by five ambiguously placed transformations, the placements of which depend upon the optimization routine employed: 1.1 (nasal process of premaxilla narrow, 5/24 of one step ACCTRAN), 7.1 (tubercle present on anterolateral portion of postorbital, 2/24 of one step ACCTRAN), 25.1 (posterolingual process of coronoid angled posterolaterally at approximately 45 degrees, fixed ACCTRAN), 43.1 (posterior coracoid fenestrae absent, 8/24 of one step DELTRAN), and 58.1 (postfemoral mite pocket present, fixed DELTRAN). Finally, this stem may be further supported by as many as 12 unpolarized characters: 8.0 (parietal roof not constricted posteriorly), 9.0 (supratemporal processes tapered), 13.0 (maxilla–palatine articulation in the form of a low, rounded arch), 21.1 (posterior process of the ectopterygoid crest absent), 23.0 (angular does not extend anteriorly beyond the fourth dentary tooth [counting forward] and rarely extends beyond the posteriormost tooth), 37.0 (skull nonrugose), 49.0 (supraorbital semicircles absent), 50.0 (subocular scale series includes one very elongate scale), 55.1 (gular fold without closely approximating posteromedial folds), 56.0 (supra-auricular fold horizontal), 59.0 (hemipenes large), and 82.1 (fully developed gular pattern in females). It is equally parsimonious for each of these characters to support stem E (*Crotaphytus*) depending upon their true polarity assignments.

Stem C is supported by four unambiguous synapomorphies, two of which are fixed: 5.1 (loss of a vaulted cranium) and 20.0 (angle of the quadrate processes of the pterygoid approximately 18 degrees). The polymorphic apomorphies are characters 31.1 (number of premaxillary teeth, 0.35 of one step under both ACCTRAN and DELTRAN) and 32.1 (palatine teeth present, 6/24 of one step ACCTRAN, 8/24 of one step DELTRAN). Nine more potential synapomorphies depend upon the particular optimization routine employed. All but one of these (discovered during ACCTRAN optimization data runs) were coded as missing ("?") for *G. corona*† and thus may actually represent synapomorphies for stem D: 11.1 (septomaxillae slender and elongate, fixed), 15.1 (angle of jugal along anteroventral border of orbit approximately 90 degrees, 12/24 of one step), 24.1 (posterior mylohyoid foramen posterior to apex of coronoid, 2/24 of one step), 41.1 (one rather than two xiphisternal ribs, 3/24 of one step), 42.0 (scapular notch absent, 5/24 of one step), 53.1 (femoral pores of approximately equal size in males and females, fixed), 60.1 (females attain larger adult SVL than males, fixed), and 87.1 (territoriality absent, fixed). Finally, 25.2 (posterolingual process of the coronoid angled posteroventrally at approximately 45 degrees) may represent a fixed synapomorphy for this node (fixed DELTRAN).

Stem D is supported by one unambiguous synapomorphy: 1.1 (nasal process of premaxilla long and slender, 19/24 of one step ACCTRAN, fixed DELTRAN). It may be further supported by as many as nine ambiguous (DELTRAN) characters including six of the characters (with the same frequency values) discussed under stem C (11, 15, 24, 41, 53, 60) for which *G. corona*† was coded as missing ("?"). The three remaining potential synapomorphies include: 7.1 (tubercle on anterolateral border of postorbital, 2/24 of one step), 10.1 (supratemporal lies in a groove along ventral border of supratemporal process, 21/24 of one step), and 40.1 (autotomic fracture planes absent, 4/24 of one step).

Stem E (*Crotaphytus*) is supported by 24 unambiguous synapomorphies, 12 of which are fixed including: 19.1 (paraoccipital processes extend posterior to the occipital condyle), 27.1 (lateral process of the surangular present as a large protuberance), 33.1 (pterygoid tooth patch curls posterolaterally), 34.1 (ceratohyals with hook-like processes on proximal, medial edge), 35.1 (second ceratobranchials more than two-thirds the length of the ceratohyals), 54.1 (skin of the distal portion of tail weakly adherent to underlying musculature), 57.1 (presence of antehumeral mite pockets), 61.1 (subadult males acquire "gravid female" coloration), 66.1 (juvenile color pattern composed of white reticulations), 72.1 (acquisition of a black collar or collars outlined in white), 88.1 (lateral tail coiling behavior), and 98.3 (electromorph Tr). This stem is also supported by 12 unambiguously placed yet polymorphic transformations depending upon the optimization routine employed: 10.1 (supratemporal lies in a groove along ventral border of supratemporal process, 1/24 of one step ACCTRAN, 22/24 of one step DEL-

TRAN), 22.1 (posterior projections of the parabasisphenoid terminate at, or anterior to, the base of the sphenoccipital tubercles, fixed ACCTRAN, 23/24 of one step DELTRAN), 31.1 (number of premaxillary teeth, 0.38 of one step under both ACCTRAN and DELTRAN), 40.1 (loss of autotomic fracture planes of the caudal vertebrae, 20/24 of one step ACCTRAN, fixed DELTRAN), 42.1 (suprascapular notch present, 12/24 of one step ACCTRAN, 13/24 of one step DELTRAN), 47.1 (medial and lateral plantar tubercles contact to form an arch, 21/24 of one step ACCTRAN, 19/24 of one step DELTRAN), 76.1 (dark nuchal spots present, 19/24 of one step under both ACCTRAN and DELTRAN), 90.6 (aGPD, 0.08 of one step under both ACCTRAN and DELTRAN), 91.2 or 91.6 (6-PGD, 0.12 of one step ACCTRAN, 0.05 of one step DELTRAN), 94.2 (GOTs, 0.69 of one step under both ACCTRAN and DELTRAN), 95.2 or 95.7 (Pro, 0.58 of one step ACCTRAN, 0.56 of one step DELTRAN), and 96.6 (Est1, 0.71 of one step under both ACCTRAN and DELTRAN). Four additional potential transformations at this node are discovered only under ACCTRAN optimization including: 28.1 (moderately developed ridge present on lateral surface of the surangular, fixed), 68.1 (white component of adult dorsal pattern composed of reticulations, fixed), 85.1 (dorsal coloration golden tan, fixed), and 89.2 (H-LDH, fixed). Finally, this stem may be supported by as many as 12 transformations that could not be polarized. It is equally parsimonious for each of these characters to support stem B (*Gambelia*) and a complete listing is given under the discussion of stem B.

Stem F is supported by nine unambiguously placed transformations, four of which are fixed: 68.2 (white portion of dorsal pattern in the form of spots), 69.1 (sexual dichromatism of the dorsal color pattern), 85.4 (brown dorsal body coloration), 86.1 (saxicoly). The five unambiguous yet polymorphic apomorphies include: 24.0 (posterior mylohyoid foramen equal with apex of coronoid, 1/24 of one step under both ACCTRAN and DELTRAN), 31.0 (number of premaxillary teeth, 0.01 of one step under both ACCTRAN and DELTRAN), 51.1 (terminal supradigital scales elevated from dorsal surface of claw, 4/24 of one step under both ACCTRAN and DELTRAN), 70.1 (paired melanic keels on ventral caudal extremity, 7/24 of one step under both ACCTRAN and DELTRAN), and 77.1 (inguinal patches present, 7/24 of one step under both ACCTRAN and DELTRAN). This stem may also be supported by the following five ambiguously placed transformations, depending upon the optimization routine employed: 28.1 (ridge on lateral surface of the surangular, fixed DELTRAN), 43.1 (posterior coracoid fenestrae present, 8/24 of one step DELTRAN), 45.0 (clavicular fenestrations lost, 16/24 of one step ACCTRAN), 58.1 (postfemoral mite pockets present, fixed DELTRAN), and 89.2 (H-LDH, fixed DELTRAN).

Stem G is weakly supported by eight unambiguously placed transformations, none of which are fixed. The unambiguous, yet polymorphic apomorphies include 17.0 (palatine foramen present, 4/24 of one step under both ACCTRAN and DELTRAN), 26.0 (no bony shelf present between medial process of the surangular and ramus of mandible, 1/24 of one step under both ACCTRAN and DELTRAN), 32.1 (palatine teeth present, 2/24 of one step ACCTRAN, 5/24 of one step DELTRAN), 42.1 (suprascapular notch present, 2/24 of one step ACCTRAN, 5/24 of one step DELTRAN), 47.1 (arch formed by contact of medial and lateral plantar tubercles, 3/24 of one step under both ACCTRAN and DELTRAN), 51.1 (terminal supradigital scales elevated from dorsal surface of claws, 20/24 of one step under both ACCTRAN and DELTRAN), 70.1 (paired melanic keels present on ventral caudal extremity, 17/24 of one step under both ACCTRAN and DELTRAN), and 77.1 (inguinal patches present, 17/24 of one step under both ACCTRAN and DELTRAN). Four ambiguously placed transformations may also support this node: 22.1 (posterior projections of parabasisphenoid terminate at, or anterior to, the base of the sphenoccipital tubercles, 1/24 of one step DELTRAN), 24.0 (posterior mylohyoid foramen equal with apex of coronoid, 1/24 of one step ACCTRAN), 90.1 (aGPD, 0.08 of one step ACCTRAN), and 95.5 (Pro, 0.43 of one step ACCTRAN).

Stem H is weakly supported by one unambiguously placed polymorphic transformation: 76.0 (absence of dark nuchal spots, 13/24 of one step under both ACCTRAN and DELTRAN). This node may also be supported by two ambiguously placed transformations: 2.0 (ventral suture between vomers and premaxilla does not form a vertical ridge, 1/24 of one step ACCTRAN) and 90.1 (aGPD, 0.08 of one step, DELTRAN).

Stem I is supported by five unambiguously placed transformations, three of which are fixed: 39.1 (laterally compressed tail with dorsal and ventral fat bodies), 65.1 (off-white dorsal caudal stripe present), and 78.1 (enlarged inguinal patches in adult males). The two unambiguous yet polymorphic transformations are 31.1 (number of premaxillary teeth, 0.01 of one step under both ACCTRAN and DELTRAN) and 76.0 (dark nuchal spots lost, 6/24 of one step under both ACCTRAN and DELTRAN). Three ambiguously placed transformations may also support this node: 24.0 (posterior mylohyoid foramen equal with the apex of coronoid, 1/24 of one step ACCTRAN), 47.1 (arch formed by contact of the medial and lateral plantar tubercles, 2/24 of one step ACCTRAN), and 75.1 (ventral extent of posterior collar marking just reaches forelimb insertion, fixed ACCTRAN).

Stem J is supported by six unambiguously placed transformations, two of which represent fixed changes: 71.0 (loss of black oral melanin) and 75.2 (posterior collar terminates within antehumeral fold). The unambiguous yet polymorphic transformations include: 1.1 (nasal process of premaxilla narrow, 1/24 of one step under both ACCTRAN and DELTRAN), 32.0 (palatine teeth lost, 8/24 of one step under both ACCTRAN and DELTRAN), 44.1 (calcified cartilage anterior border of scapular fenestra absent, 3/24 of one step under both ACCTRAN and DELTRAN), and 95.4 or 95.5 (Pro, 0.11 of one step under ACCTRAN, 0.41 under DELTRAN). This stem may be further supported by two ambiguously placed transformations, both of which were discovered under ACCTRAN optimization: 89.3 (H-LDH, fixed) and 94.3 (GOTs, fixed).

Stem K is weakly supported by two unambiguously placed transformations, neither of which is fixed: 45.1 (clavicular fenestrations present, 4/24 of one step under both ACCTRAN and DELTRAN) and 83.1 (enlarged melanic axillary patches present, 18/24 of one step ACCTRAN, 15/24 of one step DELTRAN). The stem may be further supported by four ambiguously placed transformations: 70.0 (paired melanic keels absent from ventral caudal extremity, 13/24 of one step ACCTRAN), 89.3 (H-LDH, fixed DELTRAN), 94.3 (GOTs, fixed DELTRAN), and 95.4 (Pro, 0.11 of one step DELTRAN).

Stem L is supported by seven unambiguously placed synapomorphies, three of which are fixed: 73.1 (posterior collars widely separated), 75.3 (posterior collar terminates ventrally before entering the antehumeral fold), and 84.1 (olive green ventrolateral coloration present). Olive green ventrolateral coloration is not a fixed state in *C. vestigium* as northern populations are characterized by burnt-orange ventrolateral coloration. This was an artifact of the multistate character coding scheme employed in this analysis and resulted at least in part because a satisfying estimate of the frequencies of the orange and green ventrolateral conditions in *C. vestigium* could not be obtained from preserved material. The four unambiguous but polymorphic transformations include: 16.1 (acquisition of extravomerine bones, 9/24 of one step under both ACCTRAN and DELTRAN), 26.1 (bony shelf between medial process of surangular and ramus of the mandible present, 5/24 of one step under both ACCTRAN and DELTRAN), 31.1 (number of premaxillary teeth, 0.14 of one step under both ACCTRAN and DELTRAN), and 45.0 (clavicular fenestrations lost, 2/24 of one step under both ACCTRAN and DELTRAN). Finally, four ambiguously placed transformations may also support this node: 68.3 (presence of slender, transversely arranged, white dorsal stripes, fixed ACCTRAN), 91.1 (6-PGD, 0.12 of one step ACCTRAN), 95.3 (Pro, 0.29 of one step ACCTRAN), and 96.1 (Est1, 0.71 of one step ACCTRAN).

In an attempt to assess the amount of character support for each clade, bootstrap and decay index analyses were performed for the combined data set. From each of these analyses it is clear that a number of clades are rather unstable. For example, in the bootstrap analysis (Fig. 40), nodes G and H were supported in less than 50 percent of the bootstrap replications. Stems D and F also were found to be relatively weakly supported with bootstrap proportion values of 66 and 60, respectively. Despite its low bootstrap *P* value, stem F is supported by four fixed, unambiguous synapomorphies. The amount of support for stem D may be underestimated because a number of derived character states were coded as missing ("?") for the fossil taxon *G. corona*†, thus rendering these transformations ambiguous when both ACCTRAN and DELTRAN optimization routines are considered. Notably, when *G. corona*† is excluded from the analysis, the bootstrap *P* value of stem D is 100. The remaining clades appear to be well supported, given that Hillis and Bull (1993) found bootstrap proportions to be conservative estimates of stem support with P values ≥ 70 corresponding to a probability ≥ 0.95 that the corresponding clade is real.

The results of the decay index analysis (Fig. 41)

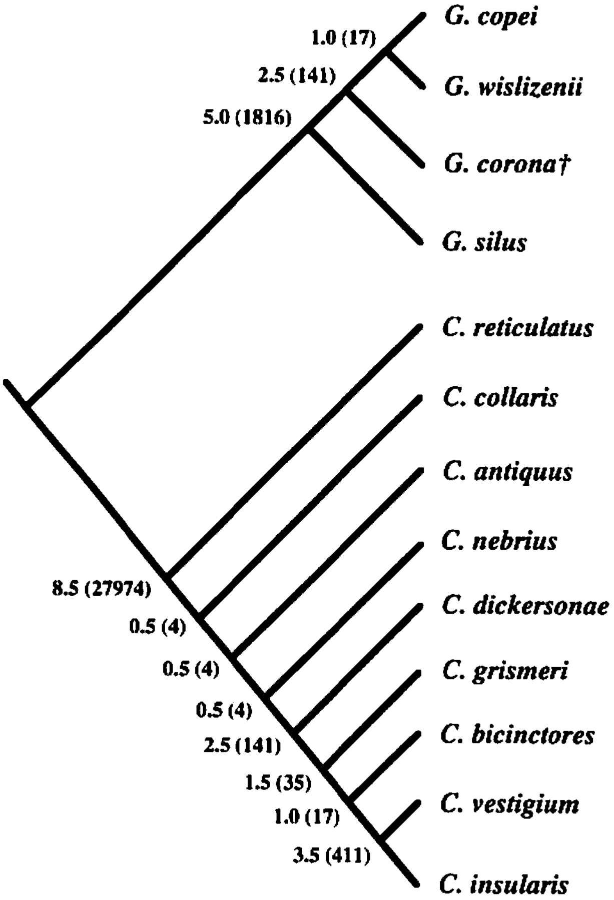

Fig. 41.—Decay index analysis: The number that is not enclosed in parentheses indicates the number of additional steps that must be considered before the node is no longer supported. The number in parentheses represents the number of equally parsimonious trees discovered when the given number of additonal steps are permitted.

agree with those of the bootstrap analysis in suggesting that a number of clades (nodes D, F, G, H, and K) are relatively unstable. Particularly well-supported clades appear to be stems B (*Gambelia*), E (*Crotaphytus*), and L (*C. insularis* + *C. vestigium*).

The allozyme and morphology data sets are not entirely consistent with one another in that the allozyme data suggest that *C. dickersonae* shares a common ancestor with *C. collaris*, *C. nebrius*, and *C. reticulatus*, whereas the morphological data suggest that *C. dickersonae* is more closely related to *C. vestigium* and *C. bicinctores*. The much smaller allozyme data set (ten characters) seems to contain less phylogenetic signal than does the morphology data set. For example, the differential between the observed g_1 and the critical g_1 value for random data is substantially greater for the morphological data set than it is for the allozyme data set (criterion suggested by J. Huelsenbeck as noted in Wiens [1995]). Nevertheless, because the topology of the single most parsimonious tree is unaffected by the inclusion or exclusion of the allozyme data, the relative phylogenetic informativeness of the allozyme data is not a critical issue. However, the bootstrap results for both the morphology-only and combined analyses should be considered when evaluating topology robustness for the single most parsimonious tree.

DISCUSSION

Comparison with Previous Hypotheses

The results of this analysis agree with those of Etheridge and de Queiroz (1988), Frost and Etheridge (1989), and virtually every other study that has considered the systematics of this group in that *Crotaphytus* and *Gambelia* are found to be sister taxa. The intrageneric relationships also are largely consistent with previous hypotheses with some notable exceptions. A major distinction between this analysis and all previous studies is the complete representation of species included here, several of which were undiscovered or were not known to be distinct lineages at the times of the previous analyses.

A phenetic analysis (Ward's Minimum Variance Cluster Analysis; Wishart, 1968) of unspecified morphological data performed by Smith and Tanner (1972) provided the first estimate of interspecific relationships within *Crotaphytus* (exclusive of *C. reticulatus*). They concluded that there were two clusters of taxa within their study group, the *collaris* complex, composed of *C. collaris* populations, and the western complex, composed of *C. bicinctores*, *C. vestigium*, *C. insularis*, and *C. dickersonae*. The two clusters are consistent with the results presented here, as both groups appear to be monophyletic.

Smith and Tanner (1974) performed another phe-

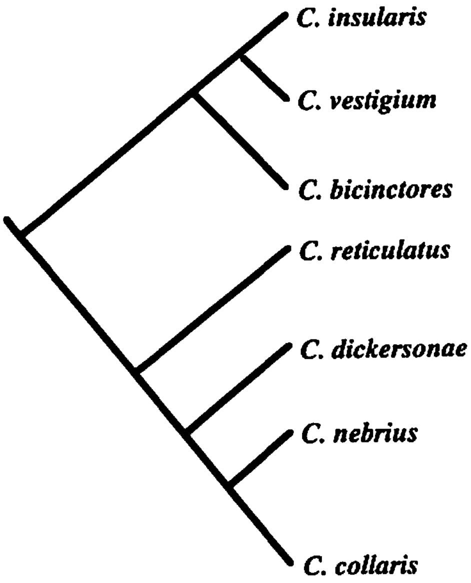

Fig. 42.—The single tree discovered by Montanucci et al. (1975) in their analysis of crotaphytid relationships.

netic analysis of *Crotaphytus* relationships (again without considering *Crotaphytus reticulatus*). The Ward's Minimum Variance Cluster Analysis (Wishart, 1968) employed morphometric and color pattern data. Their results were consistent with those of their 1972 study, although they were more specific in their assessment of relationships in this later analysis. They discussed the interspecific relationships of the western complex species and recognized two pairs of sister taxa, (*C. dickersonae* + *C. bicinctores*) and (*C. vestigium* + *C. insularis*). Their tree indicates that they were unsure whether the western complex was monophyletic or if (*C. bicinctores* + *C. dickersonae*) was actually the sister taxon of *C. collaris* (= the *collaris* complex). Their phyletic tree suggested *Gambelia* (= *G. wislizenii*) to be the sister taxon of *Crotaphytus*, and *C. reticulatus* to be the sister taxon of the remainder of *Crotaphytus*. However, data were not presented for these species and it is therefore unclear how these conclusions were reached. The phylogenetic conclusions of this analysis agree in most respects with those of the present study except in the placement of *C. dickersonae*, which was found to be the sister taxon of *C. grismeri*, *C. bicinctores*, *C. vestigium*, and *C. insularis* in this analysis.

Montanucci et al. (1975) performed the first cladistic analysis of *Crotaphytus*, utilizing 12 allozyme, discrete morphological, and morphometric characters. Their analysis of these data (using the Wagner program, Kluge and Farris, 1969) resulted in the tree depicted in Figure 42. This tree is similar to those discovered here in the placement of *C. bicinctores* as the sister taxon of (*C. vestigium* + *C. insularis*). However, their tree differs from the trees discovered here in the placement of *C. dickersonae* as the sister taxon of (*C. nebrius* + *C. collaris*), in the placement of *C. reticulatus* as the sister taxon of this group, and in placing (*C. bicinctores* (*C. vestigium* + *C. insularis*)) as the sister taxon of (*C. reticulatus* (*C. dickersonae* (*C. nebrius* + *C. collaris*))). As with the previous analyses, several taxa could not be included, such as *C. grismeri* (not yet recognized as a distinct lineage) and *C. antiquus* (yet to be discovered).

Few comparisons can be drawn between the results of this analysis and those of previous studies regarding the phylogenetic relationships of *Gambelia*. Those previous workers who recognized *G. silus* as a distinct species generally assumed it to be the sister taxon of *G. wislizenii*. Only Norell (1989) attempted to elucidate the phylogenetic relationships of *Gambelia* and he was primarily interested in the position of *G. corona*†. Although Norell (1989) described a number of useful characters, he was unable to provide phylogenetic resolution. A distinction between this analysis and several others relates to the evolution of *G. silus*. Some previous workers suggested that *G. silus* may have evolved as recently as 11,000 years ago by peripheral isolation (Montanucci, 1967, 1970; Tollestrup, 1979), although Montanucci (1970) also entertained the possibility that *G. silus* entered the valley much earlier. Regardless of the timing of the event, Montanucci (1970) suggested that differences between *G. silus* and *G. wislizenii* are examples of derived character states in *G. silus* rather than derived characteristics of *G. wislizenii*. However, most of these features, such as the presence of territoriality, a truncated snout, and sexual dimorphism wherein males are larger than females, are more parsimoniously interpreted as plesiomorphic retentions in *G. silus*. This interpretation is consistent with that of Tollestrup (1983), at least with respect to the loss of territoriality in *G. wislizenii*. Thus, it appears that *G. silus* is a relatively plesiomorphic taxon and not a recently derived offshoot of *G. wislizenii*.

It may seem counterintuitive that a narrowly distributed peripheral species such as *Gambelia silus* would be relatively plesiomorphic in comparison with a wide-ranging taxon such as *G. wislizenii* (plus its sister taxon, *G. copei*). However, there are examples of this phenomenon discussed in the herpetological literature. For example, Lynch (1982) found that the widely distributed species *Ceratophrys cornuta* exhibits numerous autapomorphies, while its close relatives, *C. calcarata* and *C. stolzmanni* are peripherally isolated and exhibit no known autapomorphies. Wiens (1993*b*) discussed a similar situation in *Urosaurus*. *Urosaurus gadovi* has a very restricted distribution in the Balsas–Tepalcatepec valley, Michoacan, Mexico, in comparison with its widely distributed sister taxon, *U. bicarinatus*. Yet, *U. bicarinatus* is relatively derived with several autapomorphies, while *U. gadovi* is relatively plesiomorphic and has no fixed autapomorphies.

CHARACTER EVOLUTION

Several evolutionary trends in the morphology and ecology of crotaphytids can be addressed in the context of the recovered phylogeny. These include the correlation between head morphology and saurophagy, the evolution of sexual dichromatism and morphologies that appear to be display oriented, bipedalism and the evolution of morphologies associated with this form of locomotion, and the function of gravid coloration and the evolution of similar coloration in subadult males.

Head Morphology and Dietary Correlates.—Head morphology and dietary preferences appear to be related in crotaphytids. Within *Gambelia*, *G. copei* and *G. wislizenii* share the derived condition of an elongate head, while *G. silus* retains the plesiomorphic blunt-snouted condition. Several studies, particularly those of Tollestrup (1979, 1983), suggest that *G. wislizenii* preys on vertebrates much more heavily than does *G. silus* and, based on my observations of stomach contents both in the field and in museum specimens, I suggest that *G. copei* will prove to be just as reliant on vertebrates as is *G. wislizenii*. A similar correlation is apparent in *Crotaphytus*. *Crotaphytus reticulatus*, *C. collaris*, *C. nebrius*, and *C. antiquus* have relatively broad heads with blunt snouts in contrast with the narrower, more elongate heads of *C. dickersonae*, *C. grismeri*, *C. bicinctores*, *C. vestigium*, and *C. insularis* (which form a monophyletic group; Fig. 37). The majority of the published dietary studies related to *Crotaphytus* have been confined to *C. collaris*, which is primarily insectivorous (Fitch, 1956, plus numerous additional references). Examination of preserved specimens with slit bellies and the skeletal preparation of preserved and fresh material has allowed for numerous observations of stomach contents, although precise records have not been maintained. These observations suggest that the "long snout" clade specializes in vertebrate prey to a greater degree than *C. reticulatus*, *C. collaris*, *C. nebrius*, and presumably *C. antiquus*. The saurophagous species may have elongate heads to allow for faster jaw adduction and predation on fast-moving prey, whereas the short-snouted condition might be associated with more powerful jaw adduction for crushing hard-shelled prey, perhaps certain insect taxa. A detailed dietary analysis to confirm these anecdotal observations for *Crotaphytus*, followed by an analysis of the functional morphology of crotaphytids (using kinematic and strain gauge analyses to measure jaw speed and jaw adductor power) would shed much light on this situation.

The Evolution of Display-oriented Morphologies in Males.—*Gambelia* and *Crotaphytus reticulatus* essentially lack sexual dichromatism outside of the breeding season, whereas the remaining species of *Crotaphytus* are characterized by the derived condition of strong sexual dichromatism throughout the year. This is the first in a series of evolutionary modifications presumably associated with an increase in display-oriented morphologies within males. There appears to have been selection for black coloration within a number of clades, the best example of which is associated with the evolution of inguinal patches in adult males. Inguinal patches appear to have passed through the following transformation series: absent → small → large, with a reversal to the polymorphic condition observed in *C. collaris*. The common ancestor of *Crotaphytus* exclusive of *C. reticulatus* appears to have been fixed for the presence of small inguinal patches. This condition persists in *C. antiquus* and *C. nebrius*, and appears to have been elaborated upon to produce much larger inguinal patches in the common ancestor of *C. dickersonae*, *C. grismeri*, *C. bicinctores*, *C. vestigium*, and *C. insularis* (Fig. 34, 35). The inguinal region is prominently displayed by male *Crotaphytus* regardless of whether or not they have inguinal patches and this may have led first to the acquisition and then enlargement of inguinal patches. If this scenario holds true, a reversion to the polymorphic state in *C. collaris* is puzzling. Two additional examples of derived black components of the color pattern are the jet-black femoral pores of *C. reticulatus* and *C. antiquus* (Fig. 23) and the enlarged, melanic axillary patches present polymorphically in *C. collaris*, *C. nebrius*, *C. bicinctores*, *C. vestigium*, and *C. insularis*.

An additional series of evolutionary modifications that is presumably associated with male display behavior are associated with lateral tail compression in the common ancestor of *C. dickersonae, C. grismeri, C. bicinctores, C. vestigium,* and *C. insularis* (Fig. 31B, 32A–D). This character complex includes the derived acquisition of dorsal and ventral caudal fat bodies as well as modifications of the neural and haemal arches and transverse processes of the caudal vertebrae. Lateral tail compression presumably increases the apparent size of adult males in lateral view. The evolution of sexual dichromatism, the acquisition and modification of black color pattern components that are restricted to males, and the development of lateral tail compression in males each suggest an increase in the importance of male display within *Crotaphytus.*

Bipedalism.—The form of bipedalism present in *Crotaphytus* appears to be unique among iguanians (see below). Several morphological modifications within the genus appear to be related to this behavior, including the loss of autotomic fracture planes of the caudal vertebrae (character 39), the modification of the skin of the distal portion of the tail such that the skin may easily slip free (character 52; Fig. 34), the acquisition of lateral tail coiling behavior (character 87; Fig. 36), and the contact of the medial and lateral plantar tubercles of the fifth metatarsal such that they form an arch (character 45; Fig. 17). The reference to the last character requires some explanation. Snyder (1952, 1954, 1962) observed that M. gastrocnemius is usually slightly larger in bipedal lizards than in quadrupedal species. Although he emphasized that the differences in muscle mass between quadrupedal and bipedal lizards are not usually great, he noted that M. gastrocnemius was conspicuously larger in *Crotaphytus* than in any other quadrupedal or bipedal lizard that he examined (Snyder, 1962). Because M. gastrocnemius inserts on the medial and lateral plantar tubercles, it is possible that the arch structure found in *Crotaphytus* increases the surface area for insertion of this muscle.

Crotaphytus utilizes a unique form of bipedal locomotion, wherein individuals jump bipedally from rock to rock on the boulder-strewn hillsides that they inhabit. This saltatory form of bipedalism allows them to move rapidly over a complex substrate and, presumably, an individual would be at a disadvantage if it were not able to maintain a bipedal gait. Snyder (1949, 1954, 1962) found that the tail of *Crotaphytus* acts as a counterbalance during bipedal locomotion and that the removal of between 25 and 33 percent of the tail prohibits a bipedal gait for more than three to five strides, while the removal of more than 50 percent prevents bipedal locomotion for more than one step. This may have been the selective factor that lead to the loss of autotomic fracture planes in the common ancestor of *Crotaphytus.* However, the tail of *Crotaphytus* is very long and it seems likely that there would be strong selective pressure to prevent predators from capturing them by this appendage, especially given that the tail cannot be broken easily (tail breakage can still occur, but requires an intervertebral separation or a fracture of the caudal vertebra itself; Etheridge, 1967). At least two evolutionary modifications have occurred in *Crotaphytus* that appear to play a role in minimizing predation by "tail capture." First, the lateral tail-coiling behavior utilized by *Crotaphytus* when taking refuge from predators beneath rocks or surface debris, during hibernation, and when resting beneath stones appears to function as a means of keeping the tail out of the reach of potential predators. Second, the presence of loosely adherent skin over the distal approximately 20 percent of the tail allows the skin of the caudal terminus to slip off when grasped, thus providing an alternative to caudal autotomy over the portion of the tail the lizard can lose without hindering its ability to run bipedally. Once the skin is removed, the underlying vertebrae and soft tissues wither and are lost. This hypothesis for the function of the loosely adherent caudal skin is based on three separate instances in which I experienced this phenomenon while attempting to capture lizards, as well as on the observation of numerous museum specimens that lack the skin of the distal portion of the tail.

Gravid Coloration.—Gravid coloration occurs in all crotaphytid taxa and a similar color pattern develops in subadult male *Crotaphytus* (character 59). Although gravid coloration itself may be a plesiomorphic retention of Crotaphytidae, the subadult male coloration is almost certainly derived (see above). The coloration of the subadult males, which develops soon after hatching and fades just before maturity (Fitch, 1956; Rand, 1986) is virtually indistinguishable both in terms of its chromatic characteristics and in its anatomical placement and, therefore, suggests that the young males may be mimicking females in order to incur some selective benefit. In fact, the presence of this coloration in young males may provide a clue to its function both in females and in the subadult males themselves.

The presence of bright red or orange dorsal pigmentation makes gravid *Crotaphytus* conspicuous at a time when crypticity presumably would be at a premium. Therefore, it is likely that the coloration provides some form of visual signal to predators or conspecifics that provides a greater selective benefit than cost to gravid females. The behavior of reproductive females toward males changes dramatically from submissive to aggressive soon after copulation, and this corresponds with an intensification of the coloration (Fitch, 1956; Clarke, 1965; Cooper and Crews, 1988). Therefore, Clarke (1965) and Cooper (1988) suggested that gravid coloration may act as an inhibitor of male aggression. If this is the case, subadult males with red or orange coloration potentially could benefit by being allowed to forage within adult male territories without being attacked. Indeed, *Gambelia* are well known for their cannibalistic habits and such coloration in *Crotaphytus* may limit predation on subadults by adult males. Because females are generally allowed to set up territories within male territories in many territorial species (Stamps, 1977; noted in *C. collaris* by Fitch, 1956, and Yedlin and Ferguson, 1973), subadult females potentially would benefit less by bearing red or orange dorsal coloration. If this is the case in *Crotaphytus*, the presence of bright red or orange coloration in subadult females might more likely be selected against (assuming the presence of vibrant orange or red coloration leaves them more conspicuous to visually oriented predators such as raptors and loggerhead shrikes). Although this hypothesis is highly speculative, it is consistent with the idea that gravid coloration has a functional value in females on which subadult males could also capitalize.

TAXONOMIC ACCOUNTS

The following taxonomic accounts include: (1) synonymies for each taxon name, (2) phylogenetic definitions for the three clade names (Crotaphytidae, *Crotaphytus*, and *Gambelia*) following the recommendations of de Queiroz and Gauthier (1992), (3) an etymology for each taxon, (4) a general description of squamation for Crotaphytidae, (5) a more specific description of squamation for each species, (6) general descriptions of coloration in life for *Crotaphytus* and *Gambelia*, (7) more specific descriptions of coloration for each species, (8) a detailed summary of geographic distribution for the genera and species (locality data used in producing the distribution maps are available from the author upon request), (9) a discussion of natural history where appropriate, and (10) a remarks section under each species account that includes references to illustrations, as well as various additional comments. The list of published illustrations may be complete for the rarer taxa, but is certainly incomplete for wide-ranging, common species such as *C. collaris* and *G. wislizenii*. Natural history observations that are not followed by a literature citation are my own.

Crotaphytidae Smith and Brodie, 1982

Crotaphytinae Smith and Brodie, 1982:106. Type genus: *Crotaphytus* Holbrook, 1842.
Crotaphytidae Frost and Etheridge, 1989:36.

Definition.—Crotaphytidae is here defined as a node-based name for the most recent common ancestor of *Crotaphytus* and *Gambelia* and all of its descendants.

Description.—A description of the squamation of crotaphytids is given here to provide a consolidated view of those features common to the family. To prevent an unnecessary duplication of information, only variable features will be discussed under the separate species accounts. General color pattern descriptions are provided under the generic accounts of *Crotaphytus* and *Gambelia*, with more specific characterizations given under each species account.

Dorsal cephalic scales smooth, convex, polygonal, occasionally with numerous inconspicuous surface irregularities. Rostral approximately two to four times wider than high, usually rectangular in shape. Rostral bordered by two to eight postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals form a thin-walled ring, pierced centrally by external nares; nares face laterally at a slight dorsal angle; nasals separated by three to nine internasals. Frontonasals occasionally enlarged. Three or four canthals, posterior one or two wider than high; four to ten scales separate canthals of left and right sides; canthus rostralis forms prominent ridge. Supraorbital semicircles present or absent; when present some scales may fuse to form azygous frontals. Interparietal small, approximately twice as long as wide, with opalescent "eye." Parietals generally small and irregular. Supraoculars small, flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present or absent; when present not well differentiated from supraoculars. Superciliaries six to 15, extremely elongate medial scale present or absent; anterior scales with oblique sutures oriented posterodorsally, posterior scales with oblique sutures oriented anterodorsally. Palpebrals ovoid, slightly convex, may be interspersed with numerous interstitial granules. Inner ciliaries deeper than wide, outer ciliaries of upper eyelid usually projecting, anterior and posterior ones projecting slightly further than medial ones; outer ciliaries of lower eyelid larger than those of upper lid, strongly projecting, conical, with anterior and posterior scales projecting slightly further than medial ones. Preoculars, suboculars, and postoculars form an arc of four to 13 rectangular scales, second, third, or fourth scale elongate or not, all with strong superior keel, strongly concave below keel. Supralabials 11 to 18, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Supralabials followed posteriorly by a series of elongate postlabials. Lorilabials in one to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Loreals numerous, larger than adjacent lorilabials. Lower temporals small, convex, oval, often separated by interstitial granules; zone of less convex, polygonal or rounded, juxtaposed scales approximately 1.5 to two times larger than bordering upper and lower temporals, extending posteriorly from postoculars but not reaching external auditory meatus; corresponding to underlying postorbital bones. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals may or may not be separated from infralabials by sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials ten to 18, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike or flat, each scale may be separated from adjacent scales by numerous asymmetrically arranged interstitial granules. Gulars flattened and discoid in gular pouch region. Gulars within symphysial groove much smaller than surrounding scales that overlie mandibles.

Dorsal scales of neck and body very small, rounded, strongly convex, nonimbricate, each characteristically surrounded by six interstitial granules giving appearance of a six-pointed star. Median dorsal scales 1.5 to two times larger than lateral dorsal scales. Dorsals grade smoothly into ventrals, approximately 136 to 224 rows encircle body midway between forelimb and hindlimb insertions. Ventrals smooth, flat, varying from oval to rhombic in shape, approximately three to four times larger than adjacent laterals, occasionally slightly imbricate.

Tail long, cylindrical to oval over entire length or anterior one-half strongly compressed laterally. Caudals usually keeled over distal 85 percent, keeling more pronounced distally. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals present or absent; posteriorly subcaudals become progressively more distinctly keeled and often mucronate. Enlarged postanal scales in males present or absent, scales between postanal plates and cloaca extremely small compared to remaining subcaudals.

Scales in immediate vicinity of forelimb insertion minute, except for a patch of large, discoid scales at anterior forelimb articulation. Suprabrachials discoid, separated by interstitial granules, becoming larger and slightly imbricate distally; distal suprabrachials approximately two times larger than dorsal body scales. Suprabrachials grade smoothly into smaller postbrachials. Prebrachials convex, beadlike, each surrounded by six symmetrically arranged interstitial granules; prebrachials grade abruptly into smaller, convex infrabrachials. Supra-antebrachials and postantebrachials small, discoid, nonoverlapping proximally, preantebrachials slightly imbricate proximally; supra-antebrachials, preantebrachials, and postantebrachials much larger and strongly imbricate adjacent to supracarpals. Infra-antebrachials convex, smaller than adjacent preantebrachials and slightly smaller than postantebrachials. Supracarpals large, strongly imbricate, continuous with large supradigital scales. Proximal supradigitals wider than long. Infracarpals strongly imbricate, usually with three strong mucrons. Subdigital lamellae moderately imbricate, each with three to six short mucrons.

Deep postfemoral dermal mite pocket may or may not be present at hindlimb insertion. Suprafemorals small, convex, nearly equal in size to lateral dorsals, separated by numerous interstitial granules, grading into prefemorals. Prefemorals becoming more discoid, slightly imbricate and larger distally; prefemorals at knee larger than surrounding scales, five to ten times larger than suprafemorals. Prefemorals grade into smaller infrafemorals; 15 to 31 femoral pores, femoral pores extend beyond angle of knee or not, separated medially by ten to 26 granular scales. Suprafemorals grade smoothly into minute, convex, oblong postfemorals, interspersed with interstitial granules. Supratibials small, convex, grade into larger, flattened, juxtaposed posttibials and larger, similarly shaped pretibials; pretibials granular where adjacent to supratarsals. Infratibials smooth, flat, juxtaposed or weakly imbricate proximally, becoming imbricate distally, much larger than adjacent pretibials and slightly larger than posttibials. Supratarsals large, imbricate anteriorly, slightly convex, granular posteriorly. Infratarsals strongly imbricate, one to three keels per scale. Supradigital scales smooth, large, strongly imbricate. Subdigital scales imbricate, with three to seven keels, each with a terminal mucron; subdigital lamellae on fourth toe 15 to 25.

Size.—All crotaphytid species are sexually dimorphic; however, males are larger than females in some species while the reverse relationship pertains in others. Maximum adult sizes range from approximately 99 mm SVL in male *Crotaphytus grismeri* to approximately 144 mm SVL in adult female *Gambelia wislizenii.*

Crotaphytus Holbrook

Crotaphytus Holbrook, 1842:79. Type species (by original designation): *Agama collaris* Say 1823.
Leiosaurus, part—Duméril, 1856:532.
Crotaphytes—Stone and Rehn, 1903:30.

Definition.—*Crotaphytus* is defined as a node-based name for the clade stemming from the most recent common ancestor of *Crotaphytus collaris* and all species that are more closely related to that species than to *Gambelia.*

Etymology.—From the Greek *krotaphos*, referring to the side of the head or temple region; and *phyton*, a creature or animal. The name apparently refers to the hypertrophied jaw adductor musculature of these lizards.

Coloration in Life.—Dorsal body coloration is extremely variable within adult male *Crotaphytus*, ranging between cobalt blue, aquamarine, green, turquoise green, golden tan, straw yellow, brown, and gray. Females of all species except *C. reticulatus* are generally characterized by a more faded version of the color present in males of their species or by pale tan or green hues. Head coloration in males may differ from that of the body, most notably in those populations of *C. collaris* characterized by a pale yellow to fluorescent yellow head. A pattern of white reticulations is a recurring phenomenon within the genus and may be present over the entire dorsal surface of the body and limbs, as well as on the temporal and superficial mandibular regions or some subset thereof. A number of species have a dorsal body and limb pattern composed of white spots or dashes rather than net-like reticulations, and narrow, transverse dorsal bars may be present. A broad white or off-white vertebral stripe may extend from the base of the tail posteriorly for most of its length. The dorsal surface of the head may be pale-colored, with a more or less patternless surface. All *Crotaphytus* are characterized by a ventral coloration of white, off-white, or pale yellow, although additional markings may be present. Olive green, golden orange, or burnt orange ventrolateral coloration may be present in males as well. The tail may or not be bright lemon yellow in adult females or burnt orange in subadult females.

Gular coloration in adult males is highly variable with olive green, gun-barrel blue, slate gray, dark brown, dark blue, turquoise blue, yellow, or orange all characterizing the adult males of certain populations. The gular region of females is generally white or only faintly patterned. The gular coloration of adult males may or may not include a black central component. The pattern surrounding the gular region of adult males is also variable and may be composed of pale reticulations, white spots on a sky blue background, or radiating, obliquely oriented, white lines.

Black is an important color component within the genus with all species having some combination of black markings. All *Crotaphytus* except some female *C. insularis* and *C. reticulatus* have at least one pair of black collar markings and most have two pairs. The anterior and posterior collar markings are separated by a broad white bar that may or may not be complete middorsally. The anterior pair of collar markings contact ventrally through the gular fold in adult males of some species. The posterior collar markings may contact middorsally in some species as well. A pair of black spots may be present middorsally between the anterior collar markings. A pair of enlarged melanic axillary patches are variably present immediately posterior to the forelimb insertion in adult males of several species. Small or large melanic inguinal patches are also present in the adult males of several species. All *Crotaphytus* neonates are characterized by a pattern of white reticulations, some of which enclose black pigments. This pattern may or may not be retained into adulthood with little modification. The femoral pores are generally off-white to gray in color but are black in males of two species (*C. antiquus* and *C. reticulatus*). Paired, melanic keels may or may not be present on the ventral surface of the caudal extremity.

All *Crotaphytus* females develop "gravid coloration" in the form of red or orange lateral bars or spots. A similar pattern develops in subadult males of all *Crotaphytus* species.

Size.—All *Crotaphytus* exhibit sexual dimorphism wherein males are larger than females. Maximum adult sizes range from approximately 99 mm SVL in *C. grismeri* to approximately 131 mm SVL in *C. collaris* (*C. reticulatus* may reach 137 mm SVL; Montanucci, 1976).

Distribution.—Western and southcentral United States from southern Idaho and eastern Oregon southward and eastward across the southern Great Plains into Missouri, northwestern Arkansas, and extreme northwestern Louisiana, southward into southern Baja California and northcentral mainland Mexico.

Fossil Record.—Numerous Pleistocene fossils have been referred to the genus, all of which have been placed within *C. collaris* or listed as *C.* sp. (Estes, 1983). However, the localities from which some of these specimens have been collected suggest that a few of these fossils may be *C. bicinctores* and *C. nebrius* (Brattstrom, 1954; Van Devender et al., 1977; Van Devender and Mead, 1978). The fragmentary nature of most of the material renders specific identification on the basis of character evidence impossible.

Crotaphytus antiquus Axtell and Webb
(Fig. 30D)

Crotaphytus antiquus Axtell and Webb, 1995:1; fig. 1, 2. Type locality: "2.1 km N–1.7 km E Vizcaya (25°46'04"N–103°11'48"W, el 1100± m) in the Sierra Texas, Coahuila, México" (Holotype: UTEP 15900).

Etymology.—From the latin *antiquus*, meaning old or of antiquity. The name was chosen by the authors because it "incorporates (their) interpretation regarding the probable ancientness of the lizard."

Diagnosis.—*Crotaphytus antiquus* can be distinguished from all other *Crotaphytus* by the presence of gravid coloration that is limited to the anterior 15 to 50 percent of the portion of the abdomen between the forelimb and hindlimb insertions and a much larger total number of white reticulations that enclose melanic pigments. *Crotaphytus antiquus* can be distinguished further from *C. reticulatus* on the basis of its postfemoral mite pockets, sexual dichromatism of the dorsal color pattern such that females have much more subdued coloration than males, and the presence of paired, melanic mucrons on the distal subcaudal scales. It can be distinguished from all *Crotaphytus* except *C. nebrius* and western populations of *C. collaris* by its small melanic inguinal patches (patches absent in *C. reticulatus*, patches much larger and extending onto the ventral surface of the abdomen in *C. bicinctores, C. dickersonae, C. grismeri, C. insularis,* and *C. vestigium*. It can be distinguished further from all *Crotaphytus* except *C. reticulatus* by its dorsal pattern composed of a white, net-like reticulum, some of which enclose melanic pigments. It can be distinguished further from all other *Crotaphytus* except *C. reticulatus* and *C. insularis* by the the weakly defined collar markings of females. It can be distinguished further from *C. collaris* by its ventrally complete anterior collar marking in adult males. It can be distinguished further from *C. collaris* and *C. nebrius* by the presence in adult males of black pigments extending from the gular fold anteriorly into the central gular area. From *C. dickersonae, C. bicinctores, C. grismeri, C. insularis,* and *C. vestigium,* it can be distinguished further by its round, rather than laterally compressed, tail that lacks a white dorsal vertebral stripe (present in adult males of the latter five species). Finally, from *C. bicinctores, C. grismeri, C. insularis,* and *C. vestigium, C. antiquus* can be distinguished by its black buccal lining.

In addition to the characters listed above, *C. antiquus* can usually be distinguished from all other *Crotaphytus* (with the possible exception of *C. dickersonae*) on the basis of a series of scales that either completely separates or nearly separates the supraorbital semicircles. In nine of 16 *C. antiquus,* the supraorbital semicircles are separated by a row of small scales, while in six of 16 specimens, a single pair of scales is in contact, and in one specimen, two scales are in contact. In all other *Crotaphytus* except *C. dickersonae,* at least two scales of the supraorbital semicircles were in contact and this was a relatively rare condition (more than two scales in contact in six of eight *C. bicinctores,* 26 of 27 *C. collaris,* four of four *C. grismeri,* 15 of 20 *C. insularis,* nine of ten *C. nebrius,* eight of eight *C. reticulatus,* and six of seven *C. vestigium*). *Crotaphytus dickersonae* is considered most similar with respect to this character to *C. antiquus* only because one specimen had one pair of scales of the semicircles in narrow contact and three of four additional specimens had two scales in contact. Thus, the prevalent condition of *C. antiquus* (supraorbital semicircles completely separated by a row of scales) was not observed in any other species of *Crotaphytus,* although the condition may very well occur in *C. dickersonae* given a larger sample size. Thus, *C. antiquus* and other *Crotaphytus* overlap but little with respect to this feature.

Variation ($n = 19$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by three to six postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by five to six internasals. Frontonasals occasionally enlarged. Canthals three; five to seven scales separate canthals of left and right sides. Supraorbital semicircles present with 12 to 13 scales per semicircle, median scales never fuse to form azygous frontals, a series of small scales may separate the right and left supraorbital semicircles or one, or rarely two, of the scales of the semicircles may be in contact. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are 1.5 to two times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries eight to 11, extremely elongate medial scale usually present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of seven to 11 rectangular scales, second, third, or fourth scale not elongate. Supralabials 12 to 16, usually slightly longer than high. Lorilabials in two to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals sometimes separated from infralabials by sublabials; mental occasionally contacted by one or two sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 13 to 16, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 128 to 161 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical in both sexes and all age groups. Paired, median row of subcaudals may or may not be larger than adjacent subcaudals and lateral caudals. Enlarged or slightly enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 16 to 20, femoral pores do not extend beyond angle of knee, separated medially by 19 to 25 granular scales. Subdigital lamellae on fourth toe 18 to 22.

Coloration in Life.—Males of this species are characterized by a dorsal color pattern consisting of a thick white reticulum on a dark brown field. The reticulations differ from those of *C. reticulatus* in that they are thicker, and all, or nearly all, of the dorsal body reticulations enclose black pigments. A few of the forelimb and hindlimb reticulations may also enclose black pigments. As in *C. reticulatus,* the reticulum is present on nearly the entire dorsal surface including the body, the anterior half of the tail, all four limbs, the lateral surface of the head, and the superficial mandibular area. The anterior and posterior collar markings are better developed than those of *C. reticulatus* and the anterior collar is complete ventrally. Black pigmentation is present in the central gular region, as in all other adult male *Crotaphytus* except *C. collaris* and *C. nebrius.* The dorsal surface of the head is patternless, but it is not of paler coloration than the remaining dorsal surfaces, as is usually the case with *C. dickersonae, C. bicinctores, C. grismeri, C. vestigium,* and *C. insularis.* Small inguinal patches largely confined to the proximal ventral surface of the thigh are present in all adult males. The femoral pores are jet black.

The coloration of females is less vibrant than that of males. The dorsal base color is grayish brown, the white reticulum is not as bright, the dorsal reticulum encloses dark gray pigments rather than black, the femoral pore exudate is gray, and the melanic inguinal patches and black pigments of the gular fold and central gular region are absent. Females develop orange gravid coloration during the reproductive period. The one subadult female that I have examined in life had a bright yellow tail and hindlimbs.

Distribution (Fig. 43).—Known to occur in the Sierras de San Lorenzo, Texas, and Solis of extreme southwestern Coahuila, Mexico.

Fossil Record.—None.

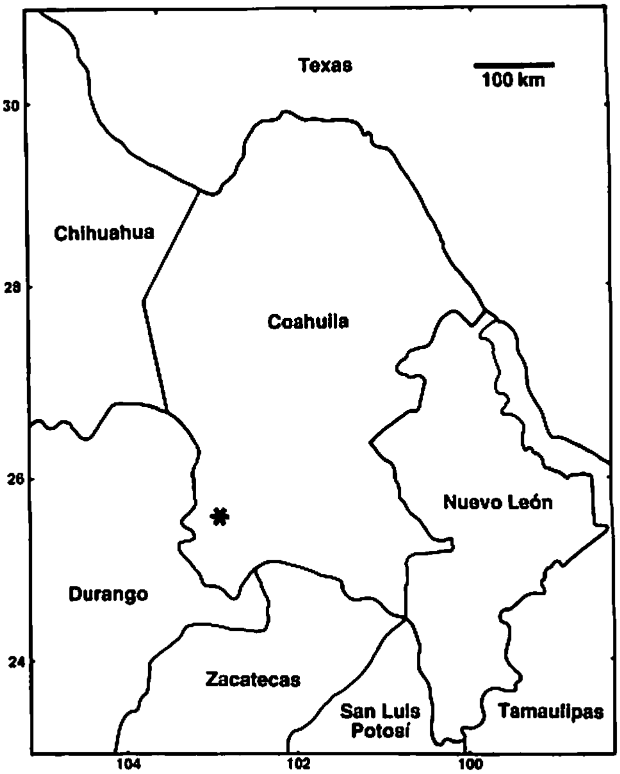

Fig. 43.—Geographic distribution of *Crotaphytus antiquus.* The asterisk indicates the location of the Sierras de San Lorenzo, Texas, and Solis in southwestern Coahuila, Mexico.

Natural History.—The following natural history observations were made on 23 and 25 June 1994. As are all *Crotaphytus* except *C. reticulatus, C. antiquus* is strongly saxicolous and usually is observed basking on large limestone rocks and outcrops. When alarmed, they generally take refuge beneath a nearby rock or under the rock upon which they were perched. The habitat at the type locality is fairly typical Chihuahuan Desert scrub with the dominant plant species being *Larrea divaricata, Jatropha dioica, Fouquieria splendens, Agave lechuguilla, Lippia graveolens, Opuntia cholla,* two unidentified species of *Opuntia* (one resembling prickly pear, the other similar in habitus to pencil cholla), and (possibly) *Echinocactus* sp. Additional reptile and amphibian species observed at the type locality include *Cnemidophorus inornatus, C. septemvittatus, Coleonyx brevis, Cophosaurus texanus, Phrynosoma modestum, Uta stansburiana, Scaphiopus couchii,* and an undescribed species of *Sceloporus* similar to *S. jarrovii cyanostictus.* A third species of *Cnemidophorus* (possibly *C. marmoratus*) is also present.

Crotaphytus antiquus are abundant and I observed more than 25 individuals in an area of about 1.5 km in length and roughly 200 m in width. This species usually runs quadrupedally, but was observed to use bipedal locomotion on occasion. They are able to take off bipedally from a standing start, as are all other *Crotaphytus* species. This species appears to be territorial, which is the case for all other *Crotaphytus* that have been studied (Fitch, 1956; Moehn, 1976; Montanucci, 1971; Sanborn and Loomis, 1979; Yedlin and Ferguson, 1973; plus numerous additional references). On 25 June 1994, I witnessed apparent territorial behavior when an adult male chased another adult male over approximately 10 m after the first male ventured into the area occupied by the second male. During the interaction, the pursuing male appeared to have its gular pouch fully depressed, a behavior that appears to be associated with aggression in all *Crotaphytus* species (Fitch, 1956; Sanborn and Loomis, 1979; personal observation).

Very little is known about the reproductive behavior of this species. However, since all but one of the females observed displayed orange gravid coloration in various stages of intensity, it is clear that the reproductive cycle includes late June. One of the females bearing gravid coloration appeared emaciated, as if she had just oviposited. No juveniles were observed, suggesting that the year's early clutches had not yet hatched. Some individuals (TNHC 53154, 53159) contained yolked ovarian follicles together with corpora lutea and distended, vascularized oviducts, suggesting that this species can produce at least two clutches in a single reproductive season. One large female (SVL = 89 mm) contained four shelled eggs, another (SVL = 89 mm) contained three shelled eggs, and four additional females contained between one and four yolked ovarian follicles, suggesting that the species has a relatively small clutch size.

The only observation made regarding feeding habits is that one adult male that was prepared as a skeleton contained the remains of an unidentified coleopteran insect.

Illustrations.—Black-and-white photographs of males and females were provided by Axtell and Webb (1995).

Crotaphytus bicinctores
Smith and Tanner
(Fig. 32A)

Crotaphytus collaris bicinctores Smith and Tanner, 1972:27; fig. 1, 2. Type locality: "Mercury Pass, Nevada Test Site, Nye Co., Nevada" (holotype: BYU 23883).

Crotaphytus insularis bicinctores—Axtell, 1972:721; fig. 2, 5b–c, 6.

Crotaphytus bicinctores—Sanborn and Loomis, 1979:105.

Etymology.—From the Latin *bi,* two, and *cinct,* banded or girdled, in reference to "the divided banding (presumably of the collar) in the Great Basin populations" (fide Tanner, personal communication, 1993).

Diagnosis.—*Crotaphytus bicinctores* can be distinguished from *C. reticulatus. C. collaris, C. nebrius,* and *C. dickersonae* by the absence of black oral melanin. It can be further distinguished from *C. reticulatus, C. collaris,* and *C. nebrius* by the presence in adult males of a strongly laterally compressed tail with a pale white dorsal caudal stripe, enlarged dark brown or black inguinal patches that extend between one-third and two-thirds of the distance between the hindlimb and forelimb insertions, and a pale tan or off-white patternless region on the dorsal surface of the head. It may be further distinguished from *C. reticulatus* as well as *C. antiquus* by a dorsal body pattern of white spots and dashes on a brown field rather than white reticulations on a gold, tan, or brown field. It may be further distinguished from *C. nebrius* by its brown dorsal coloration rather than pale tan. It may be further distinguished from *C. collaris* by the presence of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar). It may be distinguished from *C. grismeri, C. vestigium,* and *C. insularis* by the presence of broad tan or buff transverse dorsal body bands. It may be further distinguished from *C. grismeri* by the absence of a greenish tint to the white bar that separates the collars, by a pattern of white reticulations on a brown field on the forelimbs and hindlimbs rather than a pattern of yellow forelimbs with minute brown spotting on the proximal dorsal surface of the brachium and a hindlimb coloration that is nearly patternless yellow with scattered minute brown spots from the distal thigh to the distal terminus of the limb, by the absence of a pale orange tail coloration in subadult females, and by the absence of a well-defined pale tan dorsal caudal stripe in juveniles of both sexes. It may be further distinguished from *C. insularis* and *C. vestigium* by the presence of a dorsally complete or narrowly separated posterior collar rather than a posterior collar that is broadly separated dorsally or completely absent. It can be further distinguished from *C. insularis* by the presence of a relatively broad nasal process of the premaxilla, the absence of olive green ventrolateral coloration in adult males, the presence of a pattern of small white spots and dashes (occasionally transverse bands), rather than a pattern of thicker, elongate white dashes, and the absence of extravomerine bones. It can be further distinguished from *C. vestigium* by the absence of olive green or burnt orange ventrolateral coloration.

Variation ($n = 20$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by three to five postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by five to six internasals. Frontonasals occasionally enlarged. Canthals three; five to eight scales separate canthals of left and right sides. Supraorbital semicircles present with ten to 14 scales per semicircle, median scales do not fuse to form azygous frontals. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries six to 15, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of five to 13 rectangular scales, second, third, or fourth scale only rarely elongate. Supralabials 13 to 17, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in one to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals may or may not be separated from infralabials by one to three sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 12 to 18, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 144 to 200 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval in females and juveniles over entire length, anterior one-half strongly compressed laterally in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales in males present.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 16 to 21, femoral pores do not extend beyond angle of knee, separated medially by 16 to 26 granular scales. Subdigital lamellae on fourth toe 17 to 23.

Coloration in Life.—Dorsal body coloration in adult males is brown, with pale orange or peach-colored body bands. The white component of the dorsal pattern is composed of white spots and dashes on the body, and a reticulum on the tail, hindlimbs, and forelimbs. The reticulate pattern of the forelimbs may occasionally be broken into spots. Transverse body bars are absent. Reticulations are always present on the superficial mandibular and temporal regions. A broad white or off-white caudal vertebral stripe is present. The dorsal surface of the head is pale-colored, and is conspicuously patternless. Olive green or burnt orange ventrolateral coloration is lacking, although fine ventrolateral reticulations are present. The gular coloration in adult males is generally slate gray or gun-barrel blue, with a black central gular component. The peripheral gular pattern is the standard reticulate form. Anterior and posterior collar markings are always present and the posterior markings often contact middorsally. The anterior collars are complete ventrally in adult males as black pigments are present within the gular fold. A pair of black nuchal spots are not present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are variably present. Large melanic inguinal patches are always present. The femoral pores are generally off-white to gray in color. Paired, melanic keels are variably present on the ventral surface of the caudal extremity.

Females are less vividly marked than males. The dorsal coloration is grayish brown and they lack the white dorsal caudal stripe, black pigments of the gular fold, and melanic inguinal patches, axillary patches, and gular spot. Gravid females develop vivid orange or reddish lateral bars during the gravid period. The tail is not vividly colored in adult or subadult females of this species.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 111 mm) than females (maximum observed SVL = 98 mm).

Distribution (Fig. 44).—Occurs in xeric rocky habitats in southeastern and extreme northeastern Cal-

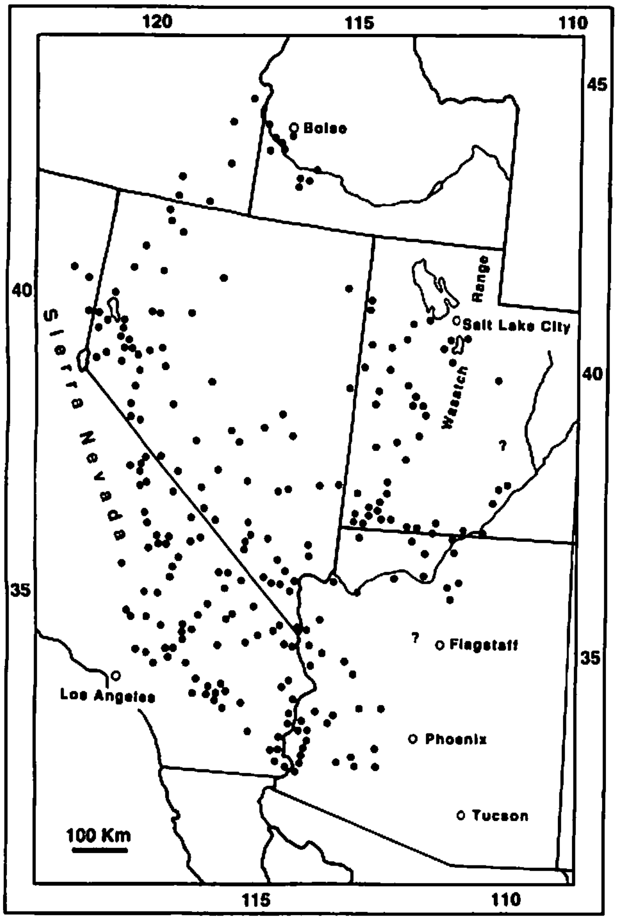

Fig. 44.—Geographic distribution of *Crotaphytus bicinctores*. The "?" near Flagstaff denotes a questionable record for the species at Williams, Arizona. The "?" in central Utah represents two records from Emery County that could not be precisely located: Nine miles W of Hanksville Highway at Nixon Uranium Mine and the Mamie Stover Incline.

ifornia, western and northern Arizona, southeastern Oregon, western Idaho, western and central Utah, and much of Nevada. In Idaho, the species occurs primarily in association with the Snake River drainage. Two additional localities in Idaho (approximately 24 km NNE of Atomic City, Butte County, and Montpelier, Bear Lake County) are not indicated on the *Crotaphytus bicinctores* distribution map (Fig. 44) but may represent relict populations. There is a series of three specimens in the Museum of Vertebrate Zoology (MVZ 43415–17) listed as collected at Cheney, Spokane County, Washington. This disjunct locality should be considered questionable until verified by additional field work.

In southwestern Arizona, the species occurs throughout the volcanic mountain ranges north of the Gila River, while *C. nebrius* occupies most of the mountain systems south of the Gila River. However, *C. bicinctores* occurs south of the Gila River near the town of Sentinel, a locality that is not occupied by *C. nebrius*. In at least two localities, *C. bicinctores* and *C. nebrius* are only narrowly separated by the Gila River. *Crotaphytus bicinctores* occurs in the Laguna Mountains which lie on the north side of the Gila River, while *C. nebrius* occurs in the Gila Mountains on the south side of the Gila River. Also, *C. bicinctores* occurs in the Gila Bend Mountains on the west shore of the Gila River, while *C. nebrius* occurs in the Buckeye Hills on the adjacent east shore. I observed a subadult *C. bicinctores* at Black Gap, Maricopa County, Arizona, a narrow pass on the western periphery of the Sauceda Mountains through which Arizona State Highway 85 passes. This observation was extremely surprising given that this area is apparently well isolated from known *C. bicinctores* populations north of the Gila Bend River and on the Sentinel Plain. If *C. bicinctores* has an established population at this locality, it is likely that *C. nebrius* and *C. bicinctores* contact somewhere in the Sauceda or Maricopa mountains. Several later attempts to find *C. bicinctores* or *C. nebrius* at this locality were unsuccessful.

In northern Arizona, *C. bicinctores* occurs within and north of the Colorado River drainage (Grand Canyon) and follows the Little Colorado River drainage as well. Over much of this area, the species occurs in close geographic proximity to *C. collaris*. Two hybrid zones between these species have been documented based on morphological and electrophoretic evidence (Axtell, 1972; Montanucci, 1983), although it seems likely that additional contact zones exist. The symbol "?" west of Flagstaff on Figure 44 represents a series of specimens (SDSNH 19474–80) that includes both *C. bicinctores* and *C. collaris*. It seems likely that the locality data for the *C. bicinctores* in this series is incorrect.

In Utah, *Crotaphytus bicinctores* occupies most of the desert mountain ranges west of the Wasatch Range and also appears to occupy the arid regions to the east of the Wasatch Range. The symbol "?" on the *C. bicinctores* map (Fig. 44) represents two localities in Emery County (9 mi W of Hanksville Highway (Hwy 24) near the Nixon Uranium Mine (BYU 16496) and the Mamie Stover Incline [BYU 20089–90]) that are represented by specimens, but for which I could not find the specific localities on topographical maps.

Fossil Record.—Pleistocene fossils collected from Rampart Cave, Arizona (Van Devender et al., 1977), Gypsum Cave, Clark County, Nevada (Brattstrom, 1954), and Smith Creek Cave, White Pine County, Nevada (Mead et al., 1982) were identified as *Crotaphytus collaris.* All fall within the current distributional range of *C. bicinctores* and therefore, on distributional grounds, may be more appropriately referred to this taxon.

Natural History.—Many anecdotal reports regarding the natural history of *Crotaphytus bicinctores* have appeared, although no general treatment of the ecology of the species has been published. The species occurs in some of the most inhospitable regions of North America including the rugged, volcanic basin and range mountains of the Sonoran, Mojave, and Great Basin deserts. It is generally restricted to rocky habitats with scant vegetation, such as alluvia, lava flows, mountain sides, canyons, and rocky plains, but occasionally may be found in peripheral areas with only limited rocky cover. I have observed individuals more than a mile away from the nearest extensive rocky habitat in association with rolling gravely hills with only occasional rocks. Their ability to inhabit such areas may allow this species to disperse across the suboptimal habitats that separate isolated desert mountain ranges, as they are known to inhabit numerous isolated mountain systems. These are diurnal lizards often seen perched atop dark volcanic rocks at temperatures over 37°C. When disturbed, they may take refuge beneath a nearby stone or bound bipedally from one rock to the next before taking refuge under a stone or in a nearby rodent hole. Although primarily saxicolous, this species occasionally may ascend small shrubs (Banta, 1967), possibly to avoid high substrate temperatures or in search of food.

The diet of this species appears to consist primarily of arthropods, including orthopterans, coleopterans, hemipterans, homopterans, hymenopterans, lepidopterans, and arachnids, as well as small vertebrates (Camp, 1916; Knowlton and Thomas, 1936; Snyder, 1972; Nussbaum et al., 1983; personal observation). *Uta stansburiana* is probably the most commonly consumed vertebrate species (Snyder, 1972; personal observation), although other recorded taxa include *Sceloporus, Cnemidophorus, Phrynosoma,* and *Xantusia vigilis* (Banta, 1960; Nussbaum et al., 1983). As do other crotaphytids, *C. bicinctores* occasionally includes plant matter in its diet (Banta, 1960).

Snyder (1972) found that adult *Crotaphytus bicinctores* in northwestern Nevada may become active as early as April 17 and large numbers may be observed in early May. I have observed adults active as early as March 19 in southwestern Arizona. In southeastern California, I have observed juveniles (probably hatched the previous season), gravid females, and adult males on May 2, indicating that mating activities probably commenced in April. Neonates have been observed in August in eastern Oregon (Brooking, 1934). Axtell (1972) hatched eggs in the laboratory on September 19. Andre and MacMahon (1980) studied the reproductive biology of *C. bicinctores* in Tule Valley, Millard County, Utah. They discovered that females reached reproductive maturity at 85 mm SVL. All females surveyed in the first week of June contained oviducal eggs and by the end of June no females contained yolked follicles or oviducal eggs. Mean clutch size was reported as 5.38 with a range of three to seven. Larger females were found to produce larger clutches of eggs.

Moehn (1976) showed that exposure to sunlight stimulates aggressive activity and despotism in captives of this species. Sanborn and Loomis (1979) discussed male display patterns. Smith (1974) noted that *C. bicinctores* may elicit a high-pitched squeal when under duress. Snyder (1972) discussed home range size and territoriality in populations adjacent to Pyramid Lake, Storey County, Nevada.

Illustrations.—A detailed black-and-white illustration of the entire animal was provided in Stebbins (1954); line drawings of the head squamation were included in Burt (1928*b*:fig. 8) and Axtell (1972). Line drawings of the dorsal and ventral color patterns were given in Smith and Tanner (1974); black-and-white photographs were provided in Axtell (1972), Pickwell (1972), Smith and Tanner (1972), and Nussbaum et al. (1983); color photographs were given by Behler and King (1979) and Sprackland (1990, 1993).

Crotaphytus collaris Say

Agama collaris Say, 1823:252. Type locality: not given; Arkansas Territory (now Oklahoma) near the Verdigris River implied (holotype: Academy of Natural Sciences of Philadelphia, now lost). Restricted type locality (Stejneger, 1890): "the Verdigris River, near its junction with the Neosho River, Creek Nation, Indian Territory"; (Stejneger and Barbour, 1917): "Verdigris River near its union with the Arkansas River, Oklahoma"; (Webb, 1970): "near Colonel Hugh Glenn's Trading Post on the east bank of the Verdigris River, about two miles above its confluence with the Arkansas River"; (Axtell, 1989*a*): Verdigris River near its union with the Arkansas River, Oklahoma.

Crotaphytus collaris—Holbrook, 1842:79; pl. 10.

Leiosaurus collaris—Duméril, 1856:532.

Crotaphytus baileyi Stejneger (syn. fide Cope, 1900), 1890:103; fig. 1, 2. Type locality: "Painted Desert, Little Colorado River, Arizona" (holotype: USNM 15821).

Crotaphytes collaris baileyi —Stone and Rehn, 1903:30.

[*Crotaphytes collaris collaris*]—Stone and Rehn, 1903:30.

Crotaphytus collaris auriceps Fitch and Tanner (syn. fide Montanucci, Axtell, and Dessauer 1975), 1951:553. Type locality: "3 1/2 mi. NNE Dewey, west side of the Colorado River, Grand County, Utah" (holotype: KU 29934).

Crotaphytus (*Crotaphytus*) *baileyi*—Weiner and Smith, 1965:187.

Crotaphytus (*Crotaphytus*) *collaris*—Weiner and Smith, 1965: 174; fig. 1–6.

Crotaphytus collaris fuscus Ingram and Tanner, 1971:23; fig. 1. Type locality: "6.5 mi. N. and 1.5 mi. W. of Chihuahua City, Chihuahua, Mexico" (holotype: BYU 16970).

Crotaphytus collaris melanomaculatus Axtell and Webb, 1995: 6; fig. 1, 2. Type locality: "25°14'10"N–103°47'W or 3.8 km S–1.7 km E Graseros on the highway to Presa Francisco Zarca, el 1250± m, Durango, México" (holotype: UTEP 15915).

Etymology.—From the Latin *collaris*, in reference to the paired black collars on the lateral and dorsal surfaces of the neck.

Diagnosis.—*Crotaphytus collaris* may be distinguished from all other species of *Crotaphytus* by the absence of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar) of adult males. It may be further distinguished from *C. reticulatus* and *C. antiquus* by the absence of a reticulate dorsal pattern in adults of both sexes and from *C. reticulatus* by the absence of jet black femoral pores in males. It may be further distinguished from *C. dickersonae, C. grismeri, C. bicinctores, C. vestigium,* and *C. insularis* by the absence in adult males of enlarged dark brown or black inguinal patches, a laterally compressed tail, a white or pale tan dorsal caudal stripe, and a pale tan or off-white patternless region on the dorsal surface of the head. It may be further distinguished from *C. grismeri, C. bicinctores, C. vestigium,* and *C. insularis* by the presence of black oral melanin.

Variation ($n = 30$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by four to six postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by four to six internasals. Frontonasals occasionally enlarged. Canthals three; five to seven scales separate canthals of left and right sides. Supraorbital semicircles present with eight to 13 scales per semicircle, median scales may fuse to form azygous frontals, especially in eastern part of range. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries six to 13, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of four to ten rectangular scales, second, third, or fourth scale not elongate. Supralabials 11 to 17, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in one to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals usually not separated from infralabials by sublabials; mental occasionally contacted by one or two sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 11 to 15, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 136 to 186 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical in both sexes and all age groups. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket usually present at hindlimb insertion. Femoral pores 15 to 24, femoral pores do not extend beyond angle of knee, separated medially by 14 to 24 granular scales. Subdigital lamellae on fourth toe 15 to 22.

Coloration in Life.—The color pattern of *Crotaphytus collaris* is extremely variable and it is probably not possible to give a complete description of the various color phases that characterize different populations of this wide-ranging species, especially given that the often vibrant coloration displayed by these lizards is quickly lost in preservative. For this reason, the following description of coloration in *C. collaris* is limited in some respects to those color morphs that I have examined firsthand.

Dorsal body coloration of adult males is extremely variable with some populations characterized by a green dorsal coloration, others by a turquoise to pale green body with a yellow head and feet, others by a pale or dark brown coloration, and still others by a gray or combination of gray and olive green. In those populations characterized by a yellow head, the intensity of the yellow pigments may range from pale to fluorescent. The white component of the dorsal pattern is retained well in preservative and is easily characterized as nearly all populations have white spots on the body with spots or reticulations present on the tail and hindlimbs. Some populations from Coahuila, Durango, Nuevo Leon, San Luis Potosi, and Zacatecas may have a dorsal pattern consisting at least in part of black spots that may or may not be surrounded by white, a pattern that is reminiscent of that of *C. antiquus* and *C. reticulatus* and potentially the result of introgression from the latter species (Montanucci, 1974). The forelimbs are generally patternless or only obscurely patterned, but may occasionally bear pale reticulations or spots. Transverse body bars are absent. Reticulations generally are confined to the superficial mandibular and temporal regions, as well as the hindlimbs and tail. A broad white or off-white caudal vertebral stripe is lacking. The dorsal surface of the head is not pale-colored, and generally is covered with spots that range in color from rust to chocolate brown. Olive green or orange ventrolateral coloration is lacking. Most of the variation in gular pattern coloration observed within *Crotaphytus* is restricted to *C. collaris*. The gular coloration observed in living adult males examined over the course of this study range between olive green, dark blue, turquoise blue, slate gray, yellow, or orange. However, a black central component is not found in this species. As stated above, the peripheral gular pattern is always composed of a white reticulated pattern. Anterior and posterior collar markings are always present and the posterior markings occasionally may contact middorsally. The anterior collars are not complete ventrally as black pigments are absent from the gular fold. A pair of black spots may be present middorsally between the anterior collar markings. A pair of enlarged melanic axillary patches are variably present immediately posterior to the forelimb insertion, although they are restricted to populations from the western portion of the species' range (Arizona). Small melanic inguinal patches are also variably present in adult males from this portion of the range. The femoral pores are generally off-white to gray in color. Paired, melanic keels may or may not be present on the ventral surface of the caudal extremity.

Female *Crotaphytus collaris* are much less conspicuously marked than males, particularly in those populations characterized by green dorsal coloration. While females may retain a green component in their pattern, it is always of a much duller hue. As in other *Crotaphytus*, the gular pattern of females is less developed. Inguinal patches, which are variably present in adult males, are lacking in females. Females develop vivid orange or reddish lateral bars during the gravid period. The tail is not vividly colored in either adult or subadult females.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 131 mm) than females (maximum observed SVL = 106 mm).

Distribution (Fig. 45).—*Crotaphytus collaris* has an extensive distribution in the western and south-central United States and northern Mexico extending from northwestern Arizona, eastern Utah, and western Colorado eastward across the southern Great Plains into Missouri, northern Arkansas, and possibly extreme northwestern Louisiana; and southward into extreme northern Sonora and northcentral mainland Mexico. Numerous isolated populations occur on the eastern periphery of its range in Missouri and Arkansas. In Texas, the eastern distributional extent of *C. collaris* is limited by the Balcones Escarpment as suitable rocky habitat does not extend east of this point. For this reason, a number of localities that lie east of the escarpment are considered questionable (FMNH 117116–18—"Cedar Creek, Bastrop Co."; USNM 12762—"Tehuacana, Limestone Co.," 14518—"Gainesville, Cooke Co."; UTA 892—"10 mi. S Dallas, Dallas Co."; see Axtell [1989*a*] for a more complete assessment of potentially erroneous localities for Texas specimens). In Mexico, *C. collaris* extends as far east as the eastern slopes of the Sierra Madre Oriental, while *C. reticulatus* occupies the flatland Tamaulipan thornscrub habitats to the immediate east. These two species approach one another closely in the vicinity of Allende, Coahuila, Mexico. In western and northern Arizona, the distributions of *C. collaris* and *C. bicinctores* abut one another and at least two hybrid zones occur (see description of the distribution of *C. bicinctores*). The questionable ("?") Colorado locality on the dot distribution map (Fig. 45) refers to a specimen (USNM 58603) from Archuleta County, Colorado, for which no specific locality data were given. The questionable ("?") locality from near the border between Tamaulipas and San Luis Potosi, Mexico, represents a locality given for *C. reticulatus* (AMNH 104448—"rte. 101, 12 mi. SW jct. with side rd. to Tula, 13 mi. NE San Luis Potosi state line"). This locality is dubious for *C. reticulatus*, but would not be unexpected for *C. collaris*.

An extremely detailed dot distribution map for *C. collaris* in Texas was provided by Axtell (1989*a*).

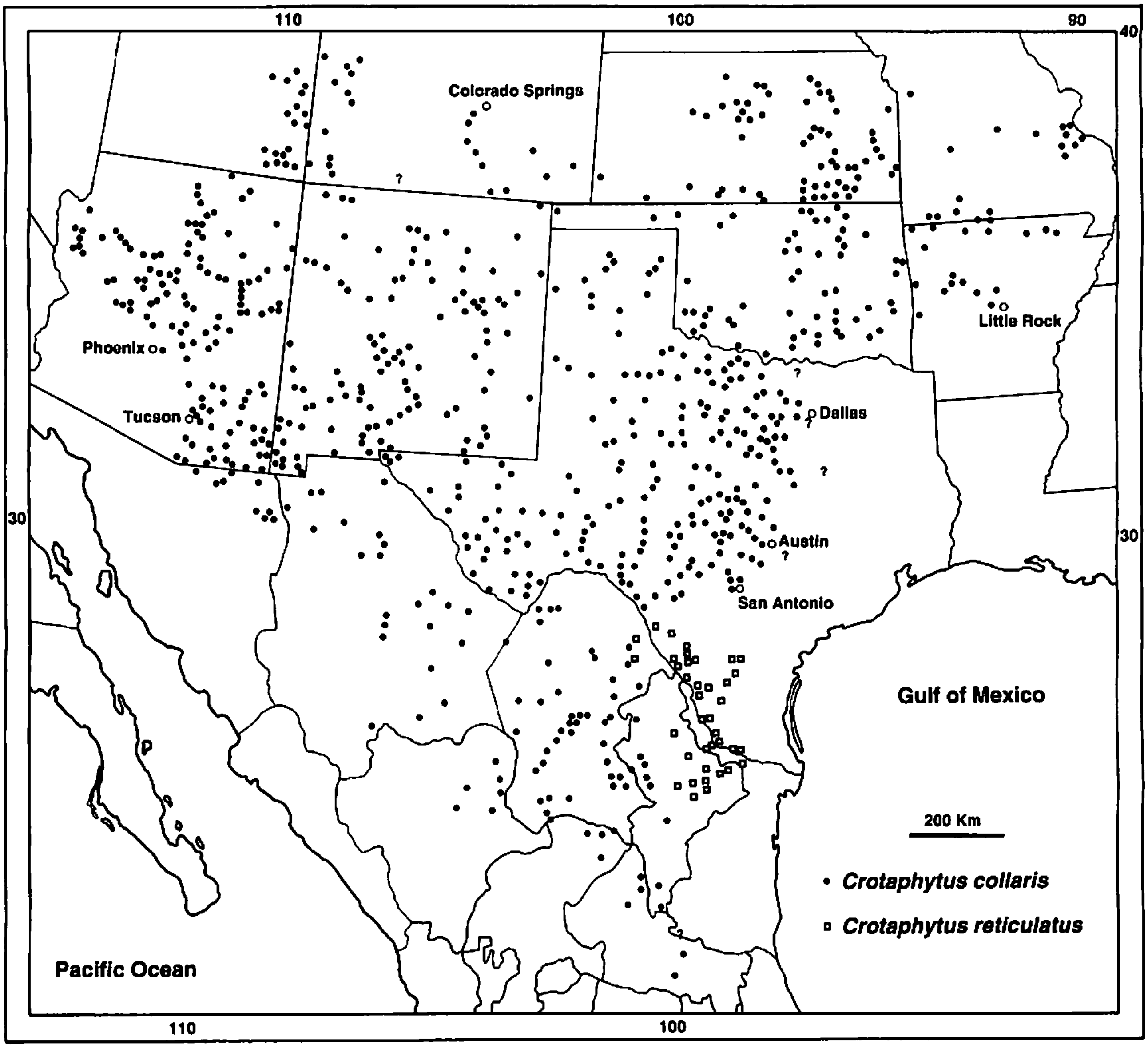

Fig. 45.—Geographic distribution of *Crotaphytus collaris* and *C. reticulatus*. The "?" in southern Colorado denotes a specimen without precise locality data from Archuleta County. The "?"s along the eastern periphery of *C. collaris'* range in Texas represent dubious localities that lie east of the Balcones Escarpment. The "?" locality from near the border between Tamaulipas and San Luis Potosi, Mexico, represents a locality given for *C. reticulatus* that is dubious for this species, but would not be unexpected for *C. collaris*.

Dot distribution maps for the states of Colorado (Hammerson, 1986), Kansas (Collins, 1982), Missouri (Johnson, 1987), and Oklahoma (Webb, 1970) have also been published.

Dundee and Rossman (1989) questioned whether *C. collaris* occurs naturally in the state of Louisiana. Two specimens are known, one of which may have been accidentally introduced (Frierson, 1927), while the other was collected by D. Leslie at Boone's Landing on the Toledo Bend Reservoir southwest of Negreet, Sabine Parish (cited as a personal communication in Dundee and Rossman, 1989).

Fossil Record.—Numerous Pleistocene fossils from several western states have been referred to this taxon, including a number of fossils more reasonably referred to other species (see *C. bicinctores* and *C. nebrius* accounts). All of the fossils, with the above exceptions, fall within the current distributional limits of *C. collaris* (Estes, 1983).

Natural History.—More has been written about the natural history of this species than any other *Crotaphytus*, with the major ecological study being Fitch (1956). Numerous unpublished master's theses and Ph.D. dissertations have dealt with ecology of *C. collaris* including (but not necessarily limited to) Mosley (1963), Trauth (1974), Hipp (1977), Bontrager (1980), McAllister (1980), Rostker (1983), Malaret (1985), Rand (1986), and Uzee (1990). More specific published works have dealt with feeding (Burt, 1928*a*; Blair and Blair, 1941; McAllister and Trauth, 1982), growth (Sexton et al., 1992), endoparasites (McAllister, 1985), reproduction (Greenberg, 1945; Clark, 1946; Robison and Tanner, 1962; Cooper and Ferguson, 1972, 1973; Parker, 1973; Ferguson, 1976; Trauth, 1978, 1979; Montanucci, 1983; Ballinger and Hipp, 1985), territoriality and aggression (Greenberg, 1945; Yedlin and Ferguson, 1973; Fox and Baird, 1992), hibernation (Legler and Fitch, 1957), aquatic behavior (McAllister, 1983), and thermoregulatory behavior (Dawson and Templeton, 1963; Cothran and Hutchison, 1979) to highlight just a small sample of the vast amount of literature pertaining to this species.

Illustrations.—Numerous illustrations and photographs have appeared in publications and this list, by necessity, is not intended to be complete. Published figures include black-and-white illustrations of the entire animal (Harlan, 1835; Holbrook, 1842; Baird, 1859), head squamation (Baird, 1859; Stejneger, 1890; Cope, 1900; Burt, 1928*b*; Stebbins, 1954, Ingram and Tanner, 1971), dorsal pattern (Ingram and Tanner, 1971; Smith and Tanner, 1974), limb and preanal squamation (Cope, 1900), and skull, pectoral girdle, and pelvic girdle (Weiner and Smith, 1965). Black-and-white photographs are found in Ditmars (1920) and Van Denburgh (1922); color plates in Ditmars (1920), Webb (1970), Stebbins (1985), Dundee and Rossman (1989), and Conant and Collins (1991); color photographs in Cochran and Goin (1970), Leviton (1971), Behler and King (1979), Collins (1982), Hammerson (1986), Garrett and Barker (1987), Johnson (1987), and Sprackland (1990, 1993). Color photos showing greater roadrunners (*Geococcyx californianus*) capturing and consuming *C. collaris* were presented by Meinzer (1993).

Taxonomic Remarks.—As discussed in the Materials and Methods section, all of the subspecies of *C. collaris* except *C. nebrius* (*C. c. auriceps*, *C. c. baileyi*, *C. c. fuscus*, and *C. c. melanomaculatus*) are here synonymized with *C. collaris* because no evidence has ever been presented, nor has any been discovered here, that these taxa represent independent lineages. For example, Ingram and Tanner (1971) showed the intergrade zone between *C. c. auriceps* and *C. c. baileyi* to be larger than the range of *C. c. auriceps* itself. The only characters that have been presented that are thought to separate *C. c. baileyi* from *C. c. collaris* are the following *C. c. collaris* features: supraorbital semicircles fused medially to form one or more azygous frontal scales, gular pouch yellow-orange, a shorter broader head, and larger supraocular scales. Of these, the first two are usually considered to be the principle diagnostic features (Brown, 1903; Meek, 1905; Ruthven, 1907; Strecker, 1909; Burt, 1928*b*; plus numerous other references) and both intergrade extensively. The condition of the supraorbital semicircles varies considerably in Colorado, New Mexico, and Texas populations (Burt, 1928*b*; personal observation), which prompted Burt (1928*b*) to synonymize *C. c. baileyi* with *C. c. collaris*. The yellow-orange gular pattern of *C. c. collaris* occurs at least as far south as Fredericksburg, Gillespie County, in southern Texas. Individuals from northeastern Mexico near the south end of Don Martin Dam and the vicinity of Allende, Coahuila, and 3.2 km NW of Mina, Nuevo Leon, have a gular coloration of yellow-orange surrounded by olive green. Individuals to the south and west (for example, 30 km SSW of Cuatrocienegas) have the standard olive green gular coloration. Thus, it appears that gular coloration grades smoothly from yellow-orange to olive green in northeastern Mexico. Fitch and Tanner (1951) were the last to comment extensively on the taxonomic status of *C. c. collaris* and *C. c. baileyi*. They clearly recognized the two as pattern classes and on these grounds accorded them the rank of subspecies. With respect to *C. c. fuscus*, diagnostic characters were not presented in the type description, which was described on the basis of a distinctive discriminant function (Ingram and Tanner, 1971). Furthermore, Axtell (1989*a*) suggested that *C. c. fuscus*, *C. c. collaris*, and *C. c. baileyi* show three-way intergradation in western Texas, again implying that all three are pattern classes.

An additional problem with the current alpha taxonomy of *Crotaphytus collaris* is that the paucity or lack of adequate character support for the subspecies makes it necessary to rely on color pattern differences as a means of identification. Thus, although it was not mentioned in the original description, many herpetologists tend to think of *C. c. baileyi* as a green collared lizard with a yellow head and *C. c. fuscus* as a brown or grayish lizard (e.g., Stebbins, 1985; Conant and Collins, 1991). Unfortunately, the ranges of these subspecies, as they are currently construed, are not consistent with these color pattern concepts. *Crotaphytus c. baileyi,* whose recognized range has been fragmented over the years by the descriptions of *C. c. auriceps, C. c. fuscus,* and *C. c. melanomaculatus,* is thought to extend from western Arizona, eastward through central New Mexico, and southward through the panhandle of Texas into northcentral Mexico. The currently recognized distribution of *C. c. baileyi* makes little sense when one considers that individuals from the Big Bend region (*C. c. baileyi*) may appear phenotypically identical to those from the Organ Mountains of New Mexico (*C. c. fuscus*). Thus, the subspecies of *C. collaris* do not appear to be on separate phylogenetic trajectories and do not even seem to represent useful pattern classes.

Crotaphytus dickersonae Schmidt
(Fig. 31B, C)

Crotaphytus dickersonae Schmidt, 1922:638; fig. 2. Type locality: Isla Tiburon, Gulf of California, Mexico (holotype: USNM 64451).

Crotaphytus collaris dickersonae—Allen, 1933:7.

Crotaphytus (Crotaphytus) collaris dickersonae—Weiner and Smith, 1965:187.

Etymology.—Named in honor of Mary C. Dickerson, former curator of herpetology at the American Museum of Natural History, who studied the insular herpetofauna of the Gulf of California, Mexico.

Diagnosis.—Crotaphytus dickersonae can be distinguished from *Crotaphytus bicinctores, C. grismeri, C. insularis,* and *C. vestigium* by the presence of black oral melanin, a blue or turquoise dorsal coloration, and the absence of enlarged postanal scales in males. It may be distinguished from *C. reticulatus, C. collaris,* and *C. nebrius* by the presence in adult males of a strongly laterally compressed tail with a white or pale stripe extending vertebrally and enlarged dark brown or black inguinal patches extending between one-half and one-third of the distance between the hindlimb and forelimb insertions. It may be further distinguished from *C. reticulatus* and *C. antiquus* by the presence of a dorsal pattern of white spots on a blue or turquoise field rather than white reticulations on a gold, tan, or brown field. It may be further distinguished from *C. collaris* by the presence of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar) and the absence of enlarged postanal scales in males. It may be further distinguished from *C. nebrius* by the presence of a blue or turquoise dorsal coloration rather than tan and the absence of enlarged postanal scales in males.

Variation (n = 20).—Rostral approximately two times wider than high, usually rectangular in shape. Rostral bordered by two to four postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by four to six internasals. Frontonasals occasionally enlarged. Canthals three; four to seven scales separate canthals of left and right sides. Supraorbital semicircles present with 11 to 15 scales per semicircle, median scales do not fuse to form azygous frontals. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries eight to 12, extremely elongate medial scale absent. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of six to nine rectangular scales, second, third, or fourth scale not elongate. Supralabials 13 to 17, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in two to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals usually separated from infralabials by a pair of sublabials; sublabials occasionally absent on one or both sides. Chinshields weakly differentiated or undifferentiated. Infralabials ten to 16, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 154 to 186 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval in females and juveniles of both sexes over entire length, anterior one-half strongly laterally compressed in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales absent in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 16 to 21, femoral pores do not extend beyond angle of knee, separated medially by 17 to 25 granular scales. Subdigital lamellae on fourth toe 17 to 21.

Coloration in Life.—Dorsal body coloration in adult males is vibrant aquamarine to cobalt blue over the entire dorsal surface of the body except the distal half of the tail. There is no trace of yellow as seen in *Crotaphytus collaris.* The white component of the dorsal pattern is composed of large white spots and dashes on the body, a reticulated tail and hindlimbs, and forelimbs that are generally spotted or mottled. Transverse body bars are absent. Reticulations are always present on the superficial mandibular and temporal regions. A broad white or off-white caudal vertebral stripe is present. The dorsal surface of the head is pale-colored, and is conspicuously patternless. Olive green or burnt orange ventrolateral coloration is lacking. The gular coloration is generally slate gray with a black central gular component. The peripheral gular pattern is the standard reticulate form. Anterior and posterior collar markings are always present and the posterior markings often contact middorsally. The anterior collars are complete ventrally by way of black pigments present within the gular fold. A pair of black nuchal spots are not present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are lacking. Large melanic inguinal patches are always present. The femoral pores are generally off-white to gray in color. Paired, melanic keels are always or nearly always present on the ventral surface of the caudal extremity.

The coloration of females is much more subdued than that of males. The dorsal coloration is gray or brownish gray, rather than vivid blue, and females lack the melanic inguinal patches, black pigments in the gular fold, black central gular blotch, and white dorsal caudal stripe. Gravid females develop vivid orange or reddish lateral bars. The tail of reproductive females is bright lemon yellow.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 116 mm) than females (maximum observed SVL = 97 mm).

Distribution (Fig. 46).—Isla Tiburon in the Gulf of California, Mexico, and the desert mountains of the adjacent Sonoran coastline (Sierra Bacha and Sierra Seri) between Punta Cirio (11.6 km S Puerto Libertad) and Bahia Kino, Mexico.

Fossil Record.—None.

Natural History.—No natural history data concerning this species have been published to date. *Crotaphytus dickersonae* apparently does not deviate significantly from other saxicolous *Crotaphytus* species with respect to basic aspects of its ecology and behavior. The species is common on south and east facing slopes with sparse vegetation and scattered granitic rocks of various sizes, with lizards generally observed basking on smaller rocks on these slopes. In coastal Sonora, *C. dickersonae* were observed on hillsides characterized by the following plant species: *Bursera microphylla, Encelia farinosa, Jatropha cuneata, Pachycereus pringlei, Stenocereus thurberi, Lycium* sp., and *Harfordia macroptera.* The lizards *Uta stansburiana, Cnemidophorus tigris,* and *Callisaurus draconoides* are common on these hillsides and very likely comprise a large component of the diet of *C. dickersonae,* a species that appears to prey heavily on lizards (based on gut content observations). This species tends to occur in similar habitats on Isla Tiburon, although juveniles observed on the island were concentrated around rocky outcroppings at the summits of the low hills rather than on the scattered rocks along the lower slopes of the hills. However, this observation should not be taken to represent a general phenomenon as very little time (two days) was actually spent on the island.

Adults of both sexes were observed on 22 March 1991 in coastal Sonora and adults and juveniles were active on Isla Tiburon on 24 March 1991. Adult females did not bear gravid coloration, indicating that mating had not yet commenced. However, an adult female observed on 14 April 1992 had striking orange gravid coloration indicating that mating takes place early in the spring in this species.

Bright blue *Crotaphytus dickersonae* males stand out boldly on the pale rocks while basking and one might expect this species to be nervous and difficult to approach. This is not the case, however. Indeed, a Red-tailed Hawk (*Buteo jamaicensis*) was observed to pass directly over a basking adult male *C. dickersonae* at a height no greater than 10 m without eliciting any observable reaction from the lizard.

Illustrations.–A black-and-white illustration of the lateral and dorsal head squamation of the holotype specimen is given in Schmidt (1922). Color pho-

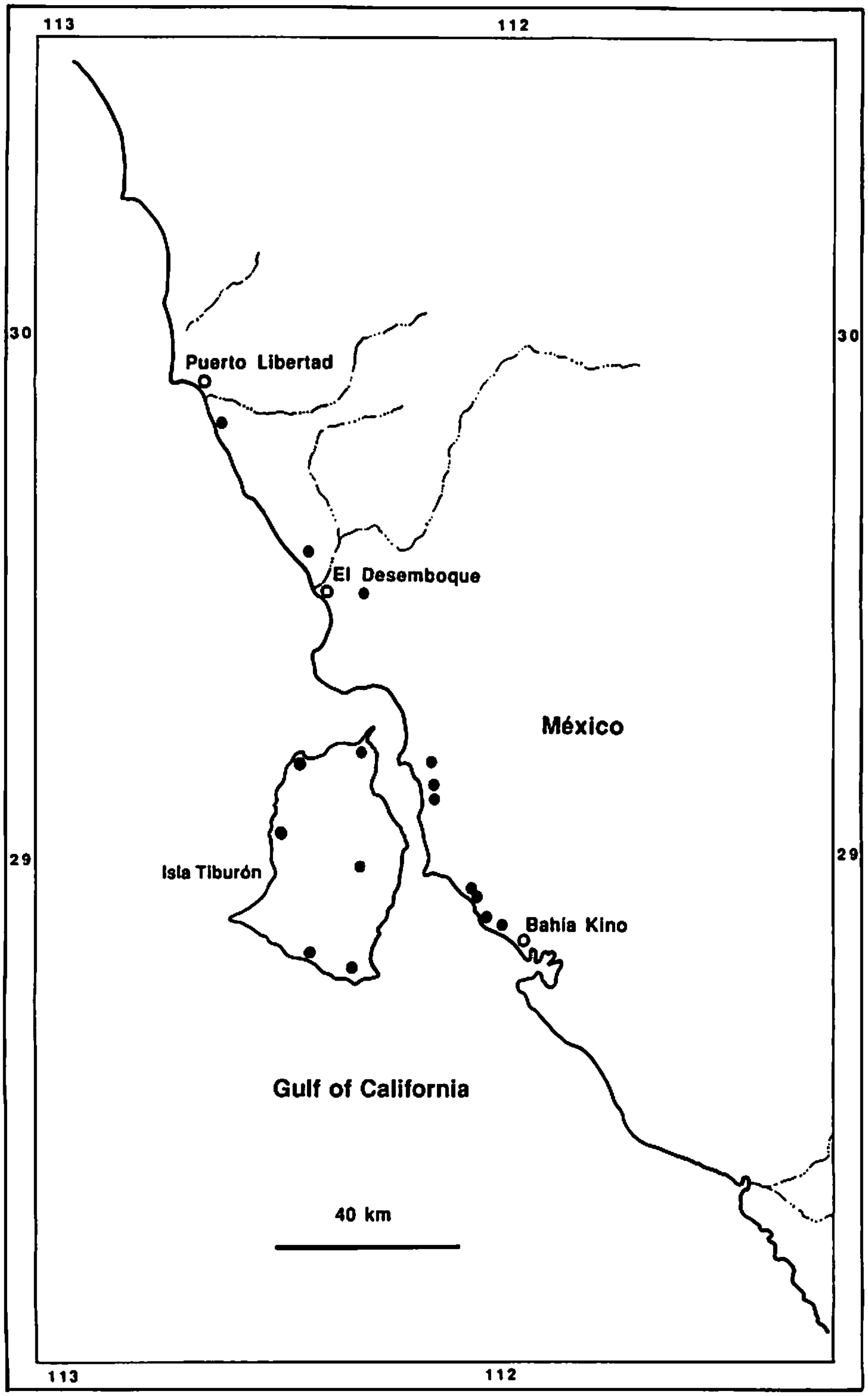

Fig. 46.—Geographic distribution of *Crotaphytus dickersonae*. The map depicts a small section of Sonoran coastline along the eastern margin of the Gulf of California.

tographs were provided in Avila (1995) and Sprackland (1993).

Crotaphytus grismeri McGuire
(Fig. 32B)

Crotaphytus grismeri McGuire, 1994:439; fig. 1. Type locality: "Cañon David, a low pass that separates the contiguous Sierra de Los Cucapas and Sierra El Mayor, approximately 2 km W Mex. Hwy. 5 on the dirt road to the sulfur mine (turnoff at km 49 S. Mexicali), Baja California, Mexico" (holotype: CES 067-629).

Etymology.—Named in honor of L. Lee Grismer, noted authority on the herpetology of Baja California.

Diagnosis.—*Crotaphytus grismeri* differs from all other *Crotaphytus* in the presence of a dull orange colored tail and hind limbs in subadult females, green pigmentation within the pale gray or white bar that separates the anterior and posterior black collars, a well-defined pale tan dorsal caudal stripe in juveniles of both sexes, a hindlimb pattern wherein the region between the middle of the thigh and its distal extremity is yellow and unmarked except for scattered minute brown spots, and in its small adult size (maximum male SVL = 99 mm, $n = 7$; $\bar{x} = 93.3$). The presence in subadult females ($n = 6$, including photographs of living individuals) of three large, lateral black spots with bold white borders may represent another diagnostic feature. *Crotaphytus grismeri* is further distinguished from *C. reticulatus, C. antiquus,* and *C. collaris* by the presence, in adult males, of large black or dark brown inguinal patches, a strongly laterally compressed tail, and a bold white dorsal caudal stripe. It differs from these species and from *C. dickersonae* in that it lacks (in both sexes) black pigmentation of the oral mucosa and in the dark brown dorsal ground color of adult males. It differs from the remaining *Crotaphytus* (*C. bicinctores, C. insularis,* and *C. vestigium*) in that the dorsal surface of the forelimb is yellow and almost without pattern, except for a small patch of minute brown spots near the forelimb insertion. It differs further from *C. insularis* and *C. vestigium* in that the posterior collar is only narrowly incomplete middorsally rather than broadly incomplete and in having a dorsal pattern of subequal white spots without transversely oriented white bars.

Variation ($n = 10$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by three to four postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by five to six internasals. Frontonasals occasionally enlarged. Canthals three; five to seven scales separate canthals of left and right sides. Supraorbital semicircles present with ten to 15 scales per semicircle, median scales sometimes fuse to form an azygous frontal. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries nine to 13, elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of seven to 13 rectangular scales, the second, third, or fourth scale only rarely elongate. Supralabials 14 to 17, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in two or three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals may or may not be separated from infralabials by a pair of sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 13 to 18, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 164 to 190 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval in females and juveniles over entire length, anterior one-half strongly compressed laterally in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 19 to 23, femoral pores do not extend beyond angle of knee, separated medially by 20 to 25 granular scales. Subdigital lamellae on fourth toe 18 to 20.

Coloration in Life.—Dorsal body coloration in adult males is brown, without pale orange or peach colored body bands. The white component of the dorsal pattern is composed of white spots and occasional dashes on the body, as well as the proximal portions of the tail and hindlimbs. Transverse body bars are absent. The forelimbs are tan with yellow blotching above and lack the white reticulations or spotting found on other *Crotaphytus*. The hindlimb is brown with white spots proximally, grading abruptly at about midthigh into yellow-tan with small light brown spots. The minute brown spots terminate proximal to the pes, which is uniform yellow-tan. The lateral surfaces of the proximal half of the tail are brown with white spots, the white component gradually expands distally such that the distal half of the tail becomes uniform pale gray. A broad white or off-white caudal vertebral stripe is present in adult males. The dorsal surface of the head is pale golden tan, and is conspicuously patternless. Reticulations are always present on the superficial mandibular and temporal regions. Olive green or burnt orange ventrolateral coloration is lacking. The gular coloration in adult males is dark blue-gray with a black central gular component. The peripheral gular pattern is the standard reticulate form. Anterior and posterior collar markings are always present. The anterior collars are complete ventrally, with black pigments extending through the gular fold. A pair of black nuchal spots are not present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are absent. Large melanic inguinal patches are always present in adult males. The femoral pores are generally off-white to gray in color. Paired, melanic keels are present on the ventral surface of the caudal extremity.

Females are less vividly marked than males. The limbs are not as distinctly yellow as in males, the head and gular markings are duller, the white dorsal caudal stripe is either absent or much less developed, and the melanic inguinal patches, ventrally complete anterior collar marking, and central gular spot are absent. Gravid females develop vivid orange or reddish lateral bars. The tail of subadult females is burnt orange in coloration.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 99 mm) than females (maximum observed SVL = 83 mm).

Distribution (Fig. 47, 48).—*Crotaphytus grismeri* is known only from the type locality and a sight record in Cañada La Palma, approximately 6 km W of El Faro. It is presumed to be restricted to the Sierra de Los Cucapas and the contiguous Sierra El Mayor, an isolated granitic mountain range in extreme northeastern Baja California, Mexico. This 80 km-long, 10 km-wide mountain range is isolated from the Sierra de Juarez of the peninsular ranges (inhabited by *C. vestigium*) to the west by Laguna Salada, a 15 km-wide flood plain that occasionally is inundated by waters from the Gulf of California. The substrate within Laguna Salada is hardpan with scattered aeolian sand. The rocky substratum required by the saxicolous *C. grismeri* is entirely absent, thus isolating this species to this mountain range.

Fossil Record.—None

Natural History.—*Crotaphytus grismeri* is saxicolous and all lizards observed at the type locality were basking on small- to medium-sized granitic rocks on rock-strewn hillsides. Lizards were observed at all levels on the hillsides, from the rocky rubble at the bases of the hills to the tops of the hillsides 100 to 200 m above (McGuire, 1994).

The activity season for the species extends at least from early March to early November. An adult male (98 mm SVL) was observed on 6 March 1993 and a juvenile male was observed on 7 November 1992. The latest date on which an adult has been observed was 12 September 1992. However, this was a gravid female and it is certain that the activity period extends at least for a few more weeks. Several gravid females were observed on 2 May and 16 May 1992 and this, together with the presence of a gravid female in early September, suggests that second clutches may be produced. Several neonates ranging in SVL between 50 and 63 mm were observed on 12 September along with the gravid female, which further supports the contention that second clutches may occur (McGuire, 1994).

Illustrations.—Color photographs of adult male, a gravid female, and a subadult female, as well as a black-and-white photo of the ventral pattern of adult males appeared in McGuire (1994).

Crotaphytus insularis
Van Denburgh and Slevin
(Fig. 32D)

Crotaphytus insularis Van Denburgh and Slevin, 1921:96. Type locality: "East coast of Angel de la Guardia Island seven miles north of Pond Island, Gulf of California, Mexico" (holotype: CAS 49151).

Crotaphytus (*Crotaphytus*) *insularis*—Weiner and Smith, 1965: 187.

Crotaphytus collaris insularis—Soulé and Sloan, 1966:140.

Crotaphytus insularis insularis—Smith and Tanner, 1972:27.

Etymology.—From the Latin *insula*, island, and *aris*, pertaining to. In reference to the insular distribution of this species.

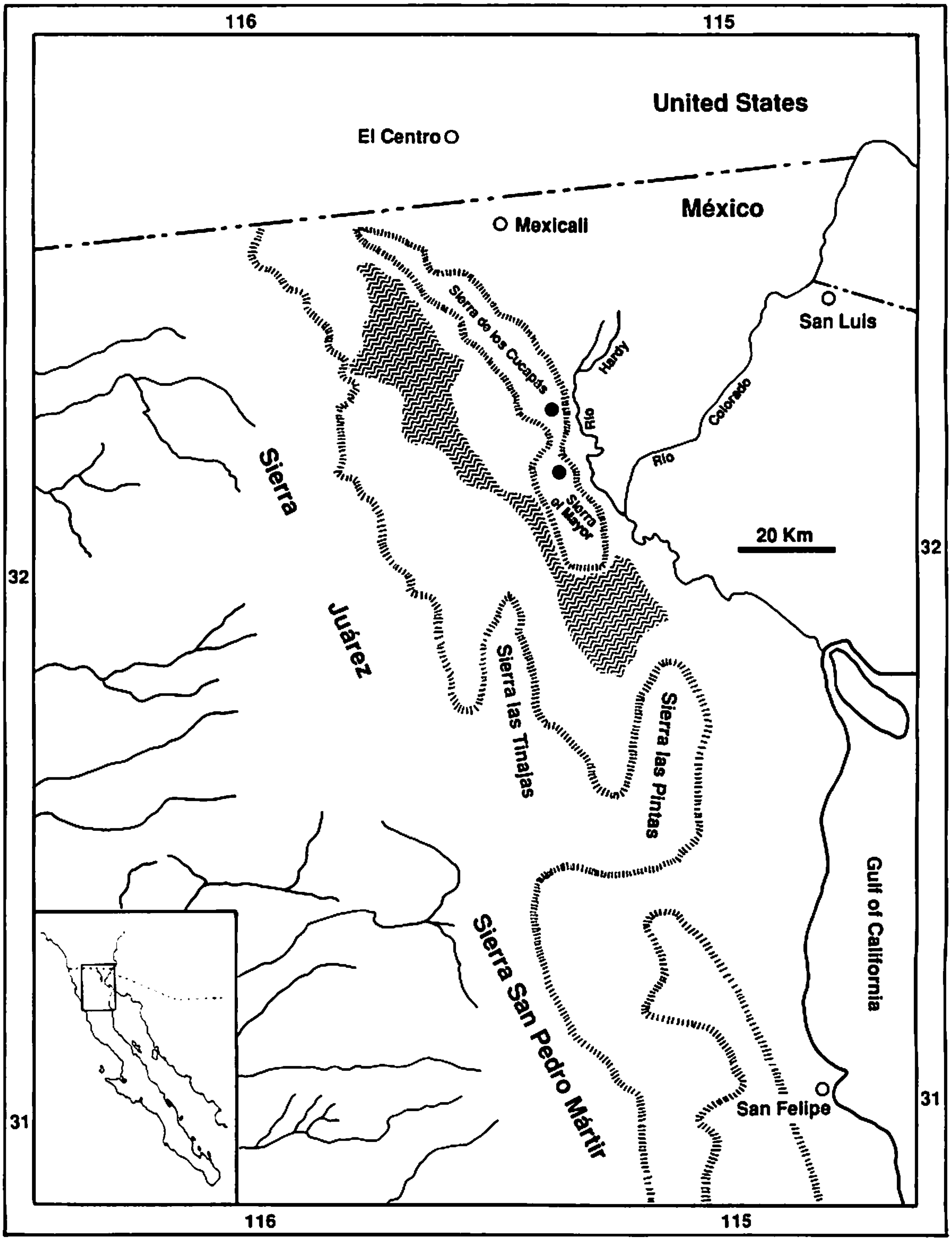

Fig. 47.—Geographic distribution of *Crotaphytus grismeri*. The wavy pattern indicates the ephemeral playa Laguna Salada. The hand-drawn hatched lines represent the borders of mountain ranges.

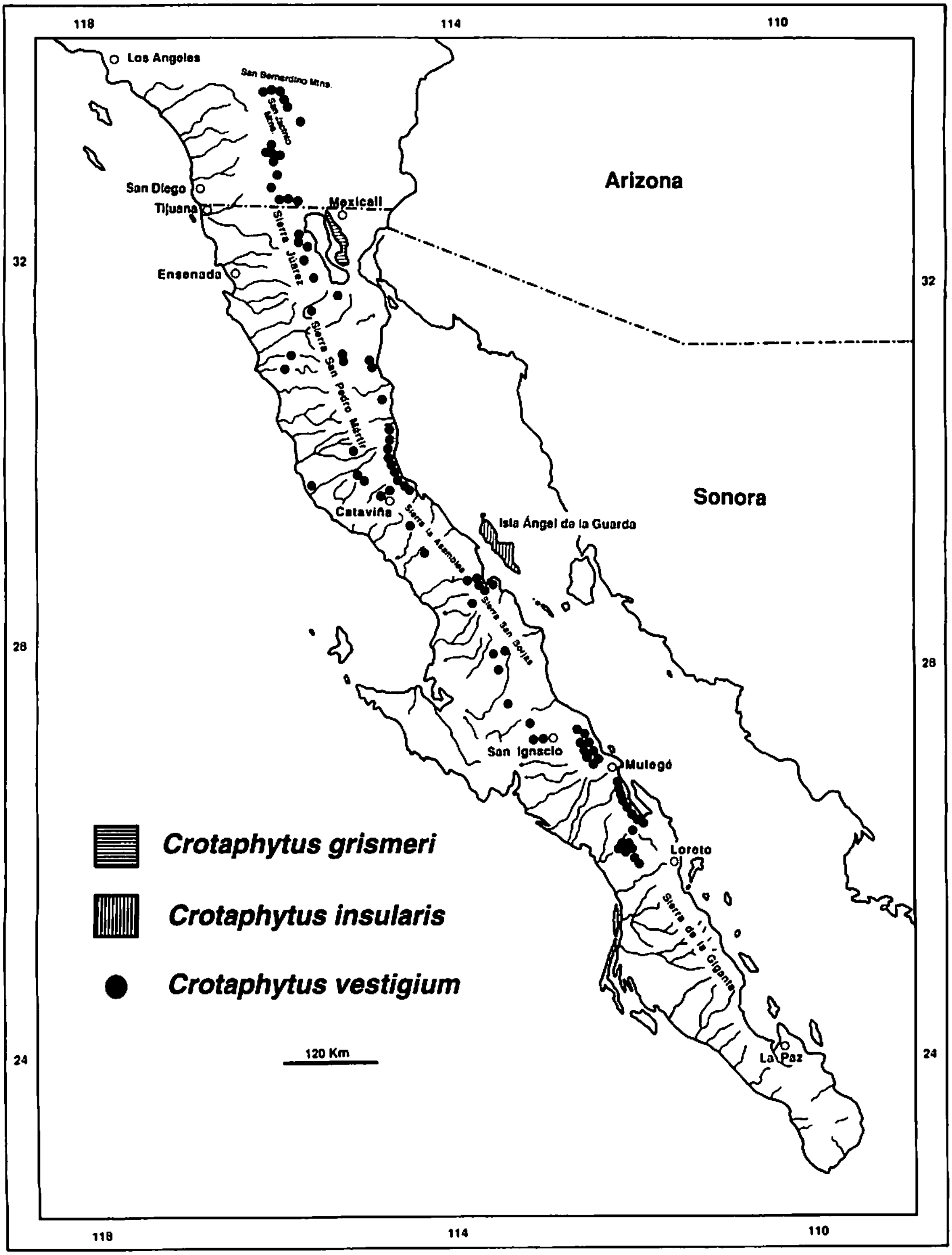

Fig. 48.—Geographic distribution of *Crotaphytus vestigium*, *C. grismeri*, and *C. insularis*.

Diagnosis.—*Crotaphytus insularis* can be distinguished from all other *Crotaphytus* by the slender and elongate nasal process of the premaxilla and its dorsal pattern of elongate white dashes, some of which may form thick, wavy transverse lines. It can be distinguished from all *Crotaphytus* except female *C. reticulatus* and occasional *C. vestigium* by the extreme reduction of the posterior collar in both sexes such that it is nearly always absent, and when present, it is extremely reduced. It can be distinguished from all but *C. vestigium* by the presence of extravomerine bones. It can be distinguished from all but some *C. vestigium* (those from north of Bahia de Los Angeles, Baja California) and some *C. collaris* by the presence in adult males of olive green ventrolateral coloration. It can be distinguished from *C. reticulatus, C. collaris, C. nebrius,* and *C. dickersonae* by the absence of black oral melanin. It can be further distinguished from *C. reticulatus, C. collaris,* and *C. nebrius* by the presence in adult males of a strongly laterally compressed tail, a white or off-white dorsal caudal stripe, a pale tan or white patternless region on the dorsal surface of the head, and enlarged dark brown or black inguinal patches (rather than the small inguinal patches of *C. nebrius* and some *C. collaris*). It can be further distinguished from *C. collaris* by the presence in adult males of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar). It can be further distinguished from *C. grismeri* by its forelimb and hindlimb patterns consisting of white reticulations on a brown field and the absence of a greenish tint in the white bar that separates the anterior and posterior collars. It can be further distinguished from *C. reticulatus* and from *C. antiquus* by the absence of the white dorsal reticulum characteristic of these species.

Variation ($n = 14$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by four to six postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by five to six internasals. Frontonasals occasionally enlarged. Canthals three; six to eight scales separate canthals of left and right sides. Supraorbital semicircles present with ten to 14 scales per semicircle, median scales do not fuse to form azygous frontals. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries eight to 13, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of six to 11 rectangular scales, second, third, or fourth scale not elongate. Supralabials 13 to 18, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in two to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals usually separated from infralabials by a pair of sublabials, occasionally only one sublabial or no sublabials present. Chinshields weakly differentiated or undifferentiated. Infralabials 11 to 17, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 166 to 206 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval in females and juveniles over entire length, anterior one-half strongly compressed laterally in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales in males present.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 19 to 23, femoral pores do not extend beyond angle of knee, separated medially by 19 to 24 granular scales. Subdigital lamellae on fourth toe 19 to 24.

Coloration in Life.—Dorsal body coloration in adult males is brown. The white component of the dorsal pattern is composed of elongate white spots and dashes on the body, with the tail, hindlimbs, and forelimbs reticulated. Transverse body bars are absent. Reticulations are always present on the superficial mandibular and temporal regions. A broad white or off-white caudal vertebral stripe is present. The dorsal surface of the head is pale-colored, and is conspicuously patternless. Olive green ventrolateral coloration is present in adult males. The gular coloration in adult males is generally slate gray with an olive green tinge. A black central gular component is present. The peripheral gular pattern is the standard reticulate form.

Anterior and posterior collar markings are only variably present with both sexes usually lacking posterior collar markings and females often lacking both the posterior and anterior collar components. When present, the posterior collar markings are reduced and do not approach one another middorsally. The anterior collars are complete ventrally in adult males, with black pigments extending through the gular fold. A pair of black nuchal spots are not present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are variably present. Large melanic inguinal patches are always present in adult males. The femoral pores are generally off-white to gray in color. Paired, melanic keels are absent from the ventral surface of the caudal extremity.

Females are less vividly marked than males. The head and gular markings are less vibrantly marked and they lack male color pattern characteristics such as the white dorsal caudal stripe and melanic inguinal patches, axillary patches, central gular patch, and ventrally complete anterior collar marking. Females develop vivid orange or reddish lateral bars during the gravid period. The tail is not vividly colored in adult or subadult females of this species.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 120 mm) than females (maximum observed SVL = 104 mm).

Distribution (Fig. 48).—Restricted to Isla Angel de La Guarda in the Gulf of California, Mexico.

Fossil Record.—None.

Natural History.—No published accounts are available regarding the natural history of *Crotaphytus insularis.* However, this species does not appear to differ markedly with respect to its behavior and ecology from its sister taxon, *C. vestigium.* Adults were observed basking on isolated volcanic rocks and a juvenile was basking on a talus slope comprised of smaller white stones. Individuals are widely spaced, which may be the result of extremely xeric conditions with very scant vegetation. Adults of both sexes and juveniles were active on 28 and 29 June 1991 and one female was observed with gravid coloration.

Illustrations.—A color photograph was provided by Sprackland (1993).

Crotaphytus nebrius
Axtell and Montanucci, **new combination**
(Fig. 31A)

Crotaphytus collaris nebrius Axtell and Montanucci, 1977:1; fig. 1. Type locality: "28°30'30"N–111°02'30"W" (14 Km by road N. Rancho Cieneguita), Sonora, Mexico" (holotype: LACM 126617).

Etymology.—From the Greek *nebrias,* meaning spotted, like a fawn. Named in reference to the fawn-like dorsal pattern of large white spots on a pale tan field.

Diagnosis.—*Crotaphytus nebrius* can be distinguished from *C. dickersonae, C. grismeri, C. bicinctores, C. vestigium,* and *C. insularis* by the absence in adult males of a laterally compressed tail, enlarged dark brown or black inguinal patches that extend between one-third and one-half the distance between the hindlimb and forelimb insertions, and a pale white dorsal caudal stripe. It can be further distinguished from *C. grismeri, C. bicinctores, C. vestigium,* and *C. insularis* by the presence of black oral melanin. It can be distinguished from *C. reticulatus* and *C. antiquus* by its dorsal color pattern of white spots on a pale tan field, rather than white reticulations on a pale tan or brown field and the absence of jet black femoral pores in males. It can be further distinguished from *C. reticulatus* by the presence in adult males of small dark brown or black inguinal patches. It can be distinguished from *C. collaris* by the presence in adult males of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar) and by the presence of burnt orange ventrolateral abdominal coloration in breeding males.

Variation ($n = 20$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by three to six postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by four to six internasals. Frontonasals occasionally enlarged. Canthals three; five to eight scales separate canthals of left and right sides. Supraorbital semicircles present with ten to 15 scales per semicircle, median scales do not fuse to form azygous frontals. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries eight to 13, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of five to ten rectangular scales, second, third, or fourth scale only rarely elongate. Supralabials 11 to 17, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in one to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals usually not separated from infralabials by sublabials; mental occasionally contacted by one or two sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 13 to 17, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 142 to 188 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical or slightly laterally compressed (oval) in both sexes and all age groups. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 17 to 22, femoral pores do not extend beyond angle of knee, separated medially by 17 to 24 granular scales. Subdigital lamellae on fourth toe 17 to 20.

Coloration in Life.—Dorsal body coloration is generally straw yellow, although this is subject to some intraspecific variation with some individuals dull tan in color. Contrary to Stebbins (1985), the anterior portion of the head may bear yellow pigments similar to those present in some populations of *C. collaris.* The white component of the dorsal pattern is composed of white spots on the body that are often roughly three times larger middorsally than they are laterally. Spots or a broken reticulum may be present on the tail and hindlimbs, while the forelimbs are generally spotted or mottled. Transverse body bars are absent. Reticulations may be absent entirely, confined to the superficial mandibular and temporal regions, or present on these regions as well as the hindlimbs below the knee. A broad white or off-white caudal vertebral stripe is lacking. The dorsal surface of the head is usually pale-colored, and is conspicuously patternless. Burnt orange ventrolateral coloration may be present in males, particularly those from the western portion of the species' distribution, and may be a form of breeding coloration. The gular coloration in males is generally slate gray or dark brown, but may be overlain with a yellow tint. A black central gular component is not present. The peripheral gular pattern is highly variable in this species, with the Tucson Mountains population characterized by the standard reticulated pattern, western populations characterized by obliquely oriented, radiating white stripes, and the remaining eastern and southern populations characterized by white spots on a sky blue background. Anterior and posterior collar markings are always present and the posterior markings may contact middorsally. The anterior collars are complete ventrally in adult males, with black pigments extending through the gular fold. A pair of black nuchal spots may be present middorsally between the anterior collar markings. A pair of enlarged melanic axillary patches are variably present immediately posterior to the forelimb insertion. Small melanic inguinal patches are always present in adult males. The femoral pores are generally off-white to gray in color. Paired, melanic keels are always present on the ventral surface of the caudal extremity, except in the Tucson Mountains populations where they are lacking in two of the three specimens examined.

Females are less vividly marked than males. The dorsal coloration is often browner than that of males. The head and gular markings are less vibrantly marked and they lack male color pattern characteristics such as the melanic inguinal patches, axillary patches, and ventrally complete anterior collar marking. Females develop vivid orange or reddish lateral bars during the gravid period. The tail is not vividly colored in adult or subadult females of this species.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 112 mm) than females (maximum observed SVL = 98 mm).

Distribution (Fig. 49).—*Crotaphytus nebrius* occurs in lowland desert and arid–tropical thornscrub mountain ranges of the Sonoran Desert where it appears to be allopatrically distributed with respect to all other *Crotaphytus.* In southwestern Arizona,

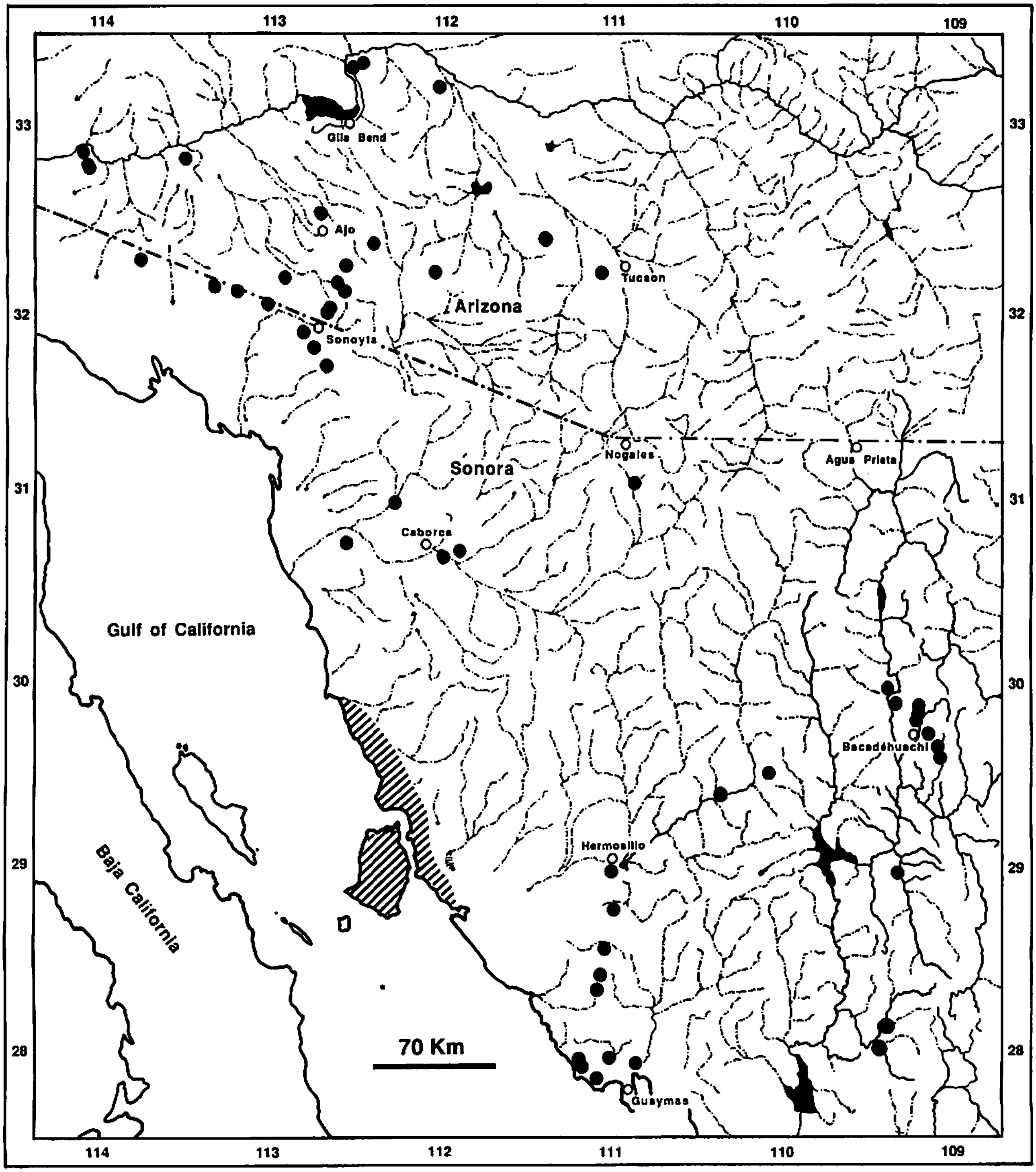

Fig. 49.—Geographic distribution of *Crotaphytus nebrius*. The cross-hatched area represents the distribution of *C. dickersonae*.

C. nebrius occurs throughout the north–south trending mountain ranges, with specimens known from the Gila, Mohawk, Little Ajo, Ajo, Pozo Redondo, Puerto Blanco, Sikort Chuapo, and Estrella mountains, as well as the Buckeye Hills. They are also known from a few mountain ranges further to the east including the Quijotoa, Silverbell, and Tucson mountains (*C. collaris* occurs on the opposite side of the Tucson Valley in the Santa Catalina Mountains). It is very likely that they occur in the remaining mountain ranges south of the Gila River, although the Baboquivari Mountains may be inhabited by *C. collaris* (Axtell and Montanucci, 1977). *Crotaphytus bicinctores* generally skirts the northern border of *C. nebrius'* range on the north side of the Gila River, but crosses the river at the Sentinel Plain, a region uninhabited by *C. nebrius*, as no Sonoran mountain ranges project northward into this area.

In Sonora, *Crotaphytus nebrius* occurs in the transversely oriented foothills that follow the United States–Mexico border along Mexican Highway 2 (the Pinacate Region). The north–south trending ranges of southwestern Arizona project northward from these foothills and probably provide the corridor through which *C. nebrius* entered these mountains. They have been collected from several mountain ranges to the south and east in northern Sonora including the Sierra Cubabi, Sierra La Gloria, Sierra El Alamo, and Sierra El Rajon. One specimen is known from either the Sierra Cibuta or Sierra El Pinto (AMNH 73758, 25.6 km S Nogales), a more eastern locality in the northern foothills of the Sierra Madre Occidental. There is a relatively large gap in the known distribution of the species between the Caborca region (Sierra El Rajon) and the Hermosillo region. However, a series of specimens are known from the foothills between Hermosillo and the Guaymas region. Finally, the remaining specimens have been taken from the foothills of the Sierra Madre Occidental, in a series of north–south trending valleys separated by presumably uninhabitable densely vegetated mountain ranges. It is likely that *C. nebrius* reached these localities by way of major river drainages entering from the south, such as the Rio Sonora and Rio Yaqui, as suitable open habitat appears to be restricted to these drainage systems.

Populations of *Crotaphytus nebrius* are only narrowly separated from those of *C. bicinctores* at two localities and in both cases the barrier that prevents contact is the Gila River. *Crotaphytus nebrius* occurs on the northern edge of the Gila Mountains and is separated from a population of *C. bicinctores* in the Laguna Mountains approximately 0.4 km to the north on the opposite side of the Gila River. Similarly, *C. nebrius* occurs on the western margin of the Buckeye Hills, while *C. bicinctores* occurs on the extreme eastern margin of the Gila Bend Mountains only a few hundred meters to the west on the opposite shore of the Gila River. Thus, *C. nebrius* may be observed on the east side of the Gillespie Bridge and *C. bicinctores* can be observed moments later on the west side.

Several questions remain regarding the distribution of *C. nebrius*. First, *C. nebrius* occurs as far north as 11.7 km N Huasabas and 19.5 km N Bacadehuachi in the Sierra Madre Occidental, while *C. collaris* is known from as far south as the Bavispe Region, approximately 60 km to the north. It is unknown whether this gap is real or an artifact of collecting. The habitat in the Huasabas and Bacadehuachi regions appears to be marginal and the presence of higher elevation mountains between this area and the Bavispe region strongly suggests that a contact zone does not exist here. However, this remains to be substantiated with additional field studies. Second, a specimen of *C. bicinctores* was observed by the author at Black Gap, Maricopa County, Arizona, a narrow pass on the western periphery of the Sauceda Mountains through which Arizona State Highway 85 passes. This observation was extremely surprising given that this area is apparently well isolated from known *C. bicinctores* populations north of the Gila Bend River and on the Sentinel Plain. If *C. bicinctores* has an established population at this locality, it is likely that *C. nebrius* and *C. bicinctores* contact somewhere in the Sauceda or Maricopa mountains. Several later attempts to find *C. bicinctores* or *C. nebrius* at this locality were unsuccessful.

Fossil Record.—Van Devender and Mead (1978) referred a maxilla and dentary from late Pleistocene deposits in the Tucson Mountains and Wolcott Peak, Pima County, Arizona, to *Crotaphytus collaris*. Van Devender et al. (1991) referred dentary, maxillae, and tooth crown material from late Pleistocene deposits in Organ Pipe Cactus National Monument to either *C. collaris* or *C. insularis*. Because the Tucson Mountains and Organ Pipe Cactus National Monument are currently inhabited by *C. nebrius*, this material probably should be referred to *C. nebrius* on distributional grounds.

Natural History.—Nothing has been published regarding the natural history of this species but I have made the following observations. *Crotaphytus nebrius* occurs in a diversity of habitats, although always in association with rocks. In the northern portion of its range it may be found in extremely xeric habitats characterized by granitic outcroppings or volcanic flows. In the southern portion of its range, it is occurs in rocky areas often with relatively dense arid–tropical thornscrub vegetation. In these areas, *C. nebrius* may be concentrated in arroyo bottoms and less vegetated stream and river valleys. In the northwestern portion of its range, the species is often found perched on granitic rocks that lay in sandy washes at the bases of rocky hillsides.

No observations have been made with respect to the feeding habits of this species although it is likely that arthropods and small lizards make up the bulk of the diet as in other *Crotaphytus* species.

The activity period for the species may extend between March and at least late September. Adult and subadult males were observed on 19 March in the Buckeye Hills, Maricopa County, Arizona, and juveniles were observed north of Guaymas, Sonora, Mexico, on 27 March. Between 15 and 19 April 1992, juveniles and subadults that apparently had just emerged from hibernation (they were still encrusted with dirt) were observed in the western foothills of the Sierra Madre Occidental and at Quijotoa, Pima County, Arizona. On the same day that the Quijotoa subadults were observed, adult males were observed just north of Ajo (Pima County) and at Mohawk, Yuma County, Arizona. Adults are active at least as late as 11 August and recently hatched neonates have been observed as late as 19 September. It seems likely that adults extend their activities at least into September and juveniles into October or November.

Reproductive behavior appears to be typical of the genus. On 14 June 1991 mating was observed in the Gila Mountains, Yuma County, Arizona. The male was observed to grasp the female by a fold of skin of the neck during coitus. The female offered no resistance and thus appeared to be fully receptive. Interestingly, the female bore fully developed gravid coloration, which is consistent with observations made by Montanucci (1965) that this coloration may not deter copulation in *Gambelia silus*, at least with females that do not display rejection behavior. It therefore seems likely that mating takes place primarily in May or June. Recently emergent neonates have been observed on 11 August in the Silverbell Mountains, Pima County, Arizona, and on 19 September in the Gila Mountains. Neonates collected in the Silverbell Mountains were as small as 44 mm SVL and the individual collected in the Gila Mountains was 42 mm SVL and still retained a small portion of the umbilicus. Thus, neonates appear to hatch out between July and/or August and September, at least in the northern portion of the range.

Illustrations.—A black-and-white photograph appears in Axtell and Montanucci (1977). A color photograph of a gravid female was provided in Sprackland (1993).

Crotaphytus oligocenicus† Holman

Crotaphytus oligocenicus Holman, 1972:1613. Type locality: "From early Oligocene, Cypress Hills Formation, north branch of Calf Creek, in L. S. 4, Sec. 8, twp. 8, range 22, W. 3rd mer., elevation 3600 ft (1100 m)" (holotype: Saskatchewan Museum of Natural History number 1444).

Etymology.—Named in reference to the time period during which these lizards lived.

Distribution.—Known only from the type locality.

Remarks.—*Crotaphytus oligocenicus*† is an extinct species of Oligocene age known only from six dentaries collected at the type locality. Because of the fragmentary nature of the type material, it cannot be determined whether this species shares any of the crotaphytid synapomorphies presented here. Thus, I agree with Estes (1983) in questioning whether this species is in fact a crotaphytid. However, given that no data were discovered in this analysis either supporting or rejecting the placement of this species within Crotaphytidae, no taxonomic rearrangements are herein suggested. A black-and-white illustration of the holotype material (a right dentary) is given in Holman (1972).

Crotaphytus reticulatus Baird
(Fig. 30C)

Crotaphytus reticulatus Baird, 1858:253. Type locality: Laredo and Ringgold Barracks, Starr County, Texas—(Smith and Taylor, 1950): "Laredo"; (Cochran, 1961) "Ringgold Barracks, Montague County, Texas"; (Montanucci, 1976): "Fort Ringgold Military Reservation (= Ringgold Barracks), Starr County, Texas" (lectotype Montanucci, 1976: USNM 2692A).

Crotaphytus (Crotaphytus) reticulatus—Weiner and Smith, 1965: 187.

Etymology.—From the Latin *reticulatus*, made like a net. In reference to the net-like dorsal and gular pattern of white reticulations present in this species.

Diagnosis.—*Crotaphytus reticulatus* can be distinguished from all other species of *Crotaphytus* except *C. antiquus* by the presence of an adult color pattern consisting of white reticulations, some of which enclose black pigmentation, and the presence of jet black femoral pores in males. It can be distinguished from *C. antiquus* by the dorsal coloration of golden tan rather than dark brown and by the presence of black pigments in only a subset of the dorsal body reticulations rather than in all or nearly all of them. It can be further distinguished from *C. collaris* by the presence of dark brown or black pigmentation in the gular fold (= ventrally complete anterior collar) in adult males. It can be further distinguished from *C. antiquus, C. nebrius, C. dickersonae, C. grismeri, C. bicinctores, C. insularis,* and

C. vestigium by the absence in adult males of small or large dark brown or black inguinal patches. It may be further distinguished from *C. dickersonae, C. grismeri, C. bicinctores, C. insularis,* and *C. vestigium* by the absence in adult males of a strongly laterally compressed tail, a white or off-white dorsal caudal stripe, and a pale tan or white patternless region on the dorsal surface of the head. It may be further distinguished from *C. grismeri, C. bicinctores, C. insularis,* and *C. vestigium* by the presence of black oral melanin.

Variation ($n = 17$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by three to six postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by five to seven internasals. Frontonasals occasionally enlarged. Canthals three; five to eight scales separate canthals of left and right sides. Supraorbital semicircles present with ten to 15 scales per semicircle, median scales do not fuse to form azygous frontals. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries seven to 13, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of seven to 12 rectangular scales, second, third, or fourth scale not elongate. Supralabials 11 to 15, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in two to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals may or may not be separated from infralabials by one or two sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials ten to 15, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 156 to 192 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval, sometimes more strongly laterally compressed in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales absent in males.

Deep postfemoral dermal mite pocket absent. Femoral pores 15 to 18, femoral pores do not extend beyond angle of knee, separated medially by 14 to 20 granular scales. Subdigital lamellae on fourth toe 18 to 22.

Coloration in Life.—Dorsal body coloration in adult males and females is golden tan. The white component of the dorsal pattern is composed of a white reticulum found over nearly the entire dorsal surface of the animal, including the body, the tail, all four limbs, and the superficial mandibular and temporal regions. Many of the white reticulations of the body (and occasionally the limbs) enclose black pigments and these black-filled hexagons are present in seven or eight transversely arranged rows. Transverse body bars are absent. A broad white or off-white caudal vertebral stripe is not present in adult males. The dorsal surface of the head is not pale colored, and may bear a mottled pattern. Olive green or burnt orange ventrolateral coloration is lacking. The gular coloration in adult males is generally slate gray or olive green and may be heavily tinged with yellow when the male breeding coloration is present. A black central gular component is present in males. Anterior and posterior collar markings are usually present in males, while only the posterior collar markings (in the form of a transverse series of black-filled reticulations) are often present in females. In both sexes, the collar markings appear to be more rudimentary than those of other *Crotaphytus* and appear to represent modified rows of transversely arranged black-filled hexagons from which black pigments have escaped and run together. When present, the posterior markings do not contact middorsally. The anterior collar markings are complete ventrally in adult males, with black pigments extending through the gular fold. A pair of black nuchal spots are generally present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are lacking. Large melanic inguinal patches are never present in adult males. The femoral pore exudate of males is jet black. Paired, melanic keels are absent from the ventral surface of the caudal extremity. Females develop vivid orange or reddish lateral bars during the gravid period. The tail is not vividly colored in adult or subadult females of this species.

Size.—This species exhibits sexual dimorphism with males reaching larger adult size (maximum observed SVL = 122 mm) than females (maximum observed SVL = 118 mm). Montanucci (1971) indicated that *Crotaphytus reticulatus* reaches a SVL of 137 mm, a much larger size than was observed in any of the material examined for this study.

Distribution (Fig. 45).—*Crotaphytus reticulatus* occurs in the Tamaulipan Biotic Province of the lower Rio Grande valley of southern Texas and adjacent Mexico (Montanucci, 1971, 1976). Montanucci (1971) provided a dot distribution map for the species as well as a verbal description of its distributional limits. Axtell (1989*b*) provided a detailed dot distribution map for the species within the confines of Texas. Montanucci (1971) stated that the western limit of the species occurred at Muzquiz, Coahuila, Mexico, which would suggest that the distributions of *C. reticulatus* and *C. collaris* overlap over an extensive area. However, Axtell (1981) found that the locality data associated with the Muzquiz specimen were erroneous. The questionable ("?") locality shown in Figure 45 from near the border between Tamaulipas and San Luis Potosi, Mexico, represents a locality given for *C. reticulatus* (AMNH 104448—"rte. 101, 12 mi. SW jct. with side rd. to Tula, 13 mi. NE San Luis Potosi state line"). This locality is dubious for *C. reticulatus*, but would not be unexpected for *C. collaris*.

Fossil Record.—None.

Natural History.—Before Montanucci's (1971) study, very little was known about the natural history of this species and his publication stands as the major contribution to this topic. *Crotaphytus reticulatus* differs in many respects from other *Crotaphytus*, particularly in that it is much less reliant on rocky habitats. Indeed, while this species will utilize rocky habitats within its range, it is often found on mesquite flats far from the nearest rocky habitat. Montanucci (1971) noted that it is not found on rocky outcroppings along the margins of bluffs (habitat that one would expect other species of *Crotaphytus* to inhabit), but that these outcroppings were occupied by *Sceloporus cyanogenys*. Montanucci (1971) refers to the preferred habitat of this species as thornbrush desert characterized by the following plant taxa: mesquite (*Prosopis glandulosa*), several species of *Acacia*, *Mimosa*, paloverde (*Cercidium macrum*), white brush (*Aloysia lycioides*), cenizo (*Leucophyllum frutescens*), and prickly pear (*Opuntia lindheimeri*). Like other *Crotaphytus*, this species prefers to bask above the surrounding substrate and this is accomplished in rockless areas by perching on fence posts (personal observation) or in the branches of mesquite trees (Montanucci, personal communication).

The natural history of *Crotaphytus reticulatus* bears a number of similarities to that of *Gambelia*. The utilization of flatland habitats with or without the presence of rocks is one notable similarity. Another is associated with their escape behavior. When alarmed, they often will run to the base of a nearby bush where they flatten themselves to the ground and remain motionless (Montanucci, 1971; personal observation), a behavior that often is observed in *G. silus* (Montanucci, 1965), *G. wislizenii*, and *G. copei*. As in the latter three species, *C. reticulatus* often will allow one to approach within one or two meters without attempting escape.

The diet of *Crotaphytus reticulatus* is similar to that of other *Crotaphytus* with arthropods (primarily orthopterans and coleopterans) making up the bulk of the diet, but with lizards (*Cnemidophorus gularis*, *Eumeces*), snakes (*Salvadora grahamiae*), and rodents (*Peromyscus*?) occasionally taken (Klein, 1951; Montanucci, 1971). As has been observed in a number of other *Crotaphytus* and *Gambelia* species, plant matter (in particular *Lycium* berries) may be consumed.

Montanucci (1971) discussed several additional aspects of *Crotaphytus reticulatus* biology including territoriality, reproduction, diel activity, seasonal activity, hatching and growth, predators, parasites, and injury.

Illustrations.—Line drawings of *Crotaphytus reticulatus* were given in Cope (1900) and Burt (1935). Black-and-white photographs were presented in Smith (1946) and Montanucci (1971, 1974). Color illustrations appear in Conant (1975) and Conant and Collins (1991). Color photographs are found in Behler and King (1979), Garrett and Barker (1987), and Sprackland (1993).

Crotaphytus vestigium Smith and Tanner
(Fig. 32C)

Crotaphytus fasciatus Mocquard, 1899:303; pl. 13, fig. 1. Type locality: "Cerro de las Palmas," Baja California, Mexico (type: none designated).

Crotaphytus fasciolatus—Mocquard (substitute name for *Crotaphytus fasciatus* Mocquard, 1899), 1903:209.

Crotaphytus insularis vestigium Smith and Tanner, 1972:29; fig. 1, 2. Type locality: "Guadelupe Canyon, Juarez Mountains, Baja California" (holotype: BYU 23338).

Crotaphytus vestigium—Collins, 1991:43.

Etymology.—From the Latin *vestigium,* a footprint, a track, a trace. In reference to the reduced collars of this species (Tanner, personal communication, 1993).

Diagnosis.—*Crotaphytus vestigium* can be distinguished from all other *Crotaphytus* except *C. insularis* and *C. reticulatus* by the presence of widely separated posterior collars. It can be distinguished from all other species of *Crotaphytus* by the presence of slender, white transverse dorsal body bars. It can be further distinguished from *C. reticulatus, C. collaris, C. nebrius,* and *C. dickersonae* by the absence of black oral melanin. It can be further distinguished from *C. reticulatus, C. collaris,* and *C. nebrius* by the presence in adult males of a strongly laterally compressed tail, a white or off-white dorsal caudal stripe, a pale tan or white patternless region on the dorsal surface of the head, and enlarged dark brown or black inguinal patches (rather than the small inguinal patches of *C. nebrius* and some *C. collaris*). It can be distinguished from *C. antiquus* and further distinguished from *C. reticulatus* in the absence of a dorsal pattern composed of a white reticulum with some or all of the reticulations enclosing black pigmentation. It can be further distinguished from *C. grismeri* by the absence of a greenish tint to the white bar that separates the anterior and posterior collars, by the hindlimb pattern consisting of white reticulations or spots on a brown field (field occasionally yellowish distal to the knee), by the presence of olive green or burnt orange ventrolateral coloration, and by its much larger maximum adult SVL. It can be distinguished from *C. insularis* by its broader nasal process of the premaxilla and its more strongly developed posterior collar.

Variation ($n = 28$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by two to five postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by three to five internasals. Frontonasals occasionally enlarged. Canthals three; five to seven scales separate canthals of left and right sides. Supraorbital semicircles present, median scales rarely fuse to form an azygous frontal. Supraoculars flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals present, not well differentiated from supraoculars. Superciliaries nine to 12, extremely elongate medial scale occasionally present. Palpebrals ovoid, slightly convex, interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of six to 11 rectangular scales, second, third, or fourth scale not elongate. Supralabials ten to 18, usually slightly longer than high except anteriormost scale, which is square or pentagonal. Lorilabials in two to three rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of large postmentals. Postmentals may or may not be separated from infralabials by one or two sublabials. Chinshields weakly differentiated or undifferentiated. Infralabials 11 to 17, square or wider than high, inferior border convex. Gulars granular, strongly convex and beadlike, each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 156 to 212 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical to oval in females and juveniles over entire length, anterior one-half strongly compressed laterally in adult males. Paired, median row of subcaudals larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales in males present.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 15 to 25, femoral pores do not extend beyond angle of knee, separated medially by 17 to 24 granular scales. Subdigital lamellae on fourth toe 15 to 25.

Coloration in Life.—Dorsal body coloration in adult males is brown. The white component of the dorsal pattern is composed of white spots and dashes on the body, a reticulated tail and hindlimbs, and forelimbs that are either reticulated, spotted, or nearly patternless. Slender, transverse body bars are present in both sexes. Reticulations are always present on the superficial mandibular and temporal regions. A broad white or off-white caudal vertebral stripe is present. The dorsal surface of the head is pale-colored, and is conspicuously patternless. Either olive green or golden orange ventrolateral coloration is present in adult males, with the former color present in individuals north of Bahia de San Luis Gonzaga, Baja California, Mexico, and the latter color present in individuals from Bahia de Los Angeles southward. The ventrolateral coloration of individuals occurring between Bahia de San Luis Gonzaga and Bahia de Los Angeles is not known. The gular coloration in adult males is generally slate gray or gun-barrel blue, with a black central gular component. The peripheral gular pattern is the standard reticulate form. Anterior collar markings are always present and posterior collar marks are only rarely lacking. The posterior markings are widely separated middorsally. The anterior collar markings are complete ventrally in adult males, with black pigments extending through the gular fold. A pair of black nuchal spots are not present middorsally between the anterior collar markings. Enlarged melanic axillary patches immediately posterior to the forelimb insertion are variably present. Large melanic inguinal patches are always present. The femoral pores are generally off-white to gray in color. Paired, melanic keels are always present on the ventral surface of the caudal extremity.

Females are less vividly marked than males. The dorsal coloration is usually gray or greenish gray. The head and gular markings are less developed and male color pattern characteristics such as the white dorsal caudal stripe, ventrally complete anterior collar markings, and melanic inguinal patches, axillary patches, and central gular spot are lacking. Gravid females develop vivid orange or reddish lateral bars. The tail is not brightly colored in adult or subadult females of this species.

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 125 mm) than females (maximum observed SVL = 98 mm).

Distribution (Fig. 48).—*Crotaphytus vestigium* inhabits the peninsular ranges and adjacent rocky habitats from the northern slope of the San Jacinto Mountains in southern California to the southern margin of the volcanic Magdalena Plain in Baja California Sur. In southern California and northern Baja California, *C. vestigium* is limited to the eastern face of the peninsular ranges. There is a gap in the peninsular ranges between the southern edge of the Sierra San Pedro Martir and the northern edge of the Sierra La Asamblea and *C. vestigium* occurs on either side of the peninsular ranges from this point southward. Furthermore, its range extends northward along the western side of the peninsular ranges from this gap to a point at least as far north as the vicinity of Rancho San Jose (Meling's Ranch) and even approaches the Pacific Coast at Mesa San Carlos (Bostic, 1971). The known southern distributional limit of *C. vestigium* is 27.7 km (by road) S of San Jose de Comondu (McGuire, 1991). It is likely that the actual distributional limit is bounded by the volcanic mesas that terminate near this locality. *Crotaphytus vestigium* apparently does not inhabit the isolated Sierra Santa Clara and Sierra Vizcaino on the Vizcaino Peninsula (Grismer et al., 1994).

Fossil Record.—None.

Natural History.—Very little has been written regarding the natural history of *Crotaphytus vestigium.* Sanborn and Loomis (1979) discussed the display patterns for this species and noted that it inhabits rocky outcroppings on the more rugged portions of the alluvial fans and mountain slopes at their San Jacinto Mountains study site. Common plant species at this locality included *Larrea tridentata, Encelia farinosa,* and *Ambrosia dumosa.* Welsh (1988) collected two individuals, one of which was found on a rocky volcanic slope in central desert scrub and the other on a granitic outcrop in coastal sage scrub. Bostic (1971) observed two individuals on Mesa San Carlos, a table-topped mountain overlooking the Pacific coast of Baja California approximately 350 km south of the United States–Mexico border. One of these individuals was foraging among large basaltic rocks along the edge of the mesa while the other was seen basking on a large basaltic outcropping on top of the mesa proper.

Crotaphytus vestigium is a denizen of desert hillsides, alluvial fans, canyons, and lava flows, always in association with rocks. They occur in some of the most xeric habitats of North America such as the eastern bases of the Sierra de Juarez and Sierra San Pedro Martir where they may be observed basking during the heat of the day. The rocky habitats in which they occur generally are characterized by scant vegetation. Common plant taxa with which *C. vestigium* is often associated include *Fouquieria splendens, F. digueti, Opuntia, Larrea tridentata, Pachycormus discolor, Bursera, Ferocactus, Pachycereus pringlei, Prosopis,* and numerous additional xerophilic species. When alarmed, this species can move with great speed over complex rocky terrain by bounding bipedally from one stone to the next, often taking refuge beneath a larger rock.

The activity season for adult *Crotaphytus vestigium* probably commences in March. Adults have been observed as early as 1 April 1992 at the foot of the Sierra La Asamblea, Baja California, and adult males, gravid females, and subadults have been found as early as 11 April 1992 on the lava flows just south of Puertocitos, Baja California. A subadult male observed in this area also had conspicuous orange bars similar to those of gravid females. On 9 April 1993 adults of both sexes as well as juveniles were observed at San Ignacio, Baja California Sur. At this time, large males already bore intense breeding coloration, while a large adult female appeared to have recently emerged from hibernation as dried mud was still adhering to the flanks and limbs.

Little is known about the predators of *Crotaphytus vestigium,* although it is likely that coachwhip snakes (*Masticophis flagellum*), raptors, Loggerhead Shrikes (*Lanius ludovicianus*), and Greater Roadrunners (*Geococcyx californianus*), all of which are common throughout the range of *C. vestigium,* probably prey on this species. An American Kestrel (*Falco sparverius*) was observed near Rosarito, Baja California, with a limp *C. vestigium* in its talons and, thus, represents at least one known predator on the species.

Illustrations.—Black-and-white photographs were presented in Smith and Tanner (1972), Axtell (1972), and Jones (1993). A black-and-white illustration was given in Mocquard (1899). Color photographs were provided by Sprackland (1990, 1993) and McGuire (1994).

Taxonomic Remarks.—In 1899, Mocquard described *Crotaphytus fasciatus* from Cerro Las Palmas, Baja California. It is clear from his description, and from the accompanying figure, that this is a juvenile *Crotaphytus vestigium,* and, as the name *fasciatus* predates that of *vestigium* by 73 years, the former name has priority. However, at the time of Mocquard's description, the name *fasciatus* was already in use as Hallowell (1852) had applied this name to a specimen of *G. wislizenii* from the sand hills at the lower end of Jornada del Muerte, New Mexico. Apparently realizing his error, Mocquard (1903) provided a substitute name for the Baja California species, giving it the name *C. fasciolatus,* but by the time Mocquard had corrected his mistake, *C. fasciatus* Hallowell had already been synonymized with *C. wislizenii* by Cope (1900). Thus, *C. fasciatus* Mocquard again became the senior synonym for the Baja California species of collared lizard. The name *C. fasciatus* has not since been applied to the Baja California population of *Crotaphytus* (sensu stricto), largely because later workers thought that Mocquard had described another synonym of *C. wislizenii.* Thus, Van Denburgh (1922) erroneously synonymized *C. fasciatus* Mocquard and *C. fasciolatus* Mocquard with *C. wislizenii.* Only Schmidt (1922) and Burt (1928*b*) recognized that Mocquard's specimen was indeed a *Crotaphytus* (sensu stricto). Over the following 50 years, the name *C. collaris* continued to be applied to this population and by the time it was recognized that the Baja California population is a distinct form, the name *fasciatus* Mocquard had long since been forgotten. Because the name *fasciatus* has not been used for more than 50 years and because the name *vestigium* has become firmly entrenched in the herpetological literature, an appeal should be made to the International Code of Zoological Nomenclature to use its plenary power to suppress the name *C. fasciatus* in order to maintain taxonomic stability.

Gambelia Baird

Crotaphytus—Baird and Girard, 1852:69.
Leiosaurus, part—Duméril, 1856:533.
Crotaphytus (*Gambelia*)—Baird, 1858:253. Type species (by monotypy): *Crotaphytus wislizenii* Baird and Girard, 1852*a*.
Gambelia—Smith, 1946:158.

Definition.—*Gambelia* is defined as a node-based name for the clade stemming from the most recent common ancestor of *Gambelia wislizenii* and all species that are more closely related to that species than to *Crotaphytus.*

Etymology.—Named in honor of William Gambel, ornithologist and pioneer naturalist of western North America in the mid-1800s.

Coloration in Life.—There is much variation in the color pattern of *Gambelia,* although much of this is geographic variation within the wide-ranging species *G. wislizenii.* Nevertheless, several components of the color pattern are found in all *Gambelia,* at least during some portion of ontogeny. For example, the color patterns of neonates are very similar in all three extant species. They are characterized by a series of transversely arranged, blood-red dorsal spots that begin on the head and continue onto the base of the tail. Each row of enlarged spots is generally comprised of four spots. Enlarged blood-red spots may extend onto the hindlimbs as well. Each transverse series of enlarged spots is separated by a pale or cream-colored transverse bar. The spots and bars continue onto the tail where the spots progressively coalesce distally, forming dark bars. The dark bars alternate with the pale bars giving the tail a banded appearance, a pattern that remains throughout ontogeny. Early in ontogeny, the blood-red color of the dorsal spotting begins to fade to a brown hue that is maintained into adulthood.

Another component of the juvenile pattern that is consistent among extant *Gambelia* are the obliquely oriented, radiating melanic bars present on the head. These have a visually disruptive effect and may play a role in camouflage (McCoy, 1967). These head markings are lost early in ontogeny.

The gular pattern of *Gambelia* is relatively consistent, with longitudinally arranged black streaks present in both sexes throughout ontogeny. *Gambelia silus* differs slightly from *G. copei* and *G. wislizenii* in that the streaks are usually fragmented leaving spots or rhombs.

Most *Gambelia* are characterized by the presence of brown dorsal spots that correspond to the blood-red dorsal spots of juveniles. The spots vary in size, density, and position within various populations and species. The spots may be fragmented or may be surrounded by ornamentation in the form of minute white spots. Many *Gambelia* also retain the juvenile crossbanding into adulthood and these crossbands are in many cases offset paravertebrally.

The dorsal base color of *Gambelia* is generally a pale shade of white, cream, or gray but may be dark brown. The ventral coloration is generally white, off-white, or a pale shade of gray or yellow.

All *Gambelia* lack sexual dichromatism, except in the case of male breeding coloration (present only in *G. silus*) and vivid orange or red female "gravid coloration," which is present in all *Gambelia.* The "gravid coloration" may be deposited in patches on the sides of the head and on the thighs, in a single or double row of spots along the flanks, and along the ventral surface of the tail.

Size.—*Gambelia silus* exhibits sexual dimorphism with males larger than females, while females attain much larger sizes than males in *G. copei* and *G. wislizenii.*

Distribution.—*Gambelia* is found in the western United States from central Idaho and eastern Oregon southward in the Great Basin through western Colorado and western Texas in the east, and through the San Joaquin Valley and eastern deserts of California in the west; southward into Mexico to western Coahuila, northern Zacatecas, eastern and central Chihuahua, central Sonora, and into the cape region of Baja California.

Fossil Record.—Numerous Pleistocene fossils have been referred to *Gambelia,* all of which were considered to be *G. wislizenii.* At least one fossil was found within the current distributional limits of *G. silus* and may therefore represent this species (Brattstrom, 1953).

Gambelia copei Yarrow
(Fig. 30B)

Crotaphytus copeii Yarrow, 1882:441. Type locality: "La Paz, Cal." (holotype: USNM 12663).
Crotaphytus copii—Garman, 1884:16.
Crotaphytus copei—Cope, 1887:34.
Crotaphytus wislizenii—Cope, 1900:255.
Crotaphytus wislizeni copei—Leviton and Banta, 1964:153.
Crotaphytus wislizeni neseotes Banta and Tanner (syn. fide Montanucci, 1978), 1968:186; fig. 1-5. Type locality: "Cedros Island, west coast of Baja California Norte, Mexico" (holotype: CAS 79872).

Etymology.—Named in honor of Edward Drinker Cope, noted American herpetologist and paleontologist.

Diagnosis.—*Gambelia copei* is diagnosed from *G. corona*† by the absence of a broad, transversely concave frontal bone, the presence of a frontoparietal suture posterior to the posterior extent of the orbits, and an elongate and slender nasal process of the premaxilla. It is diagnosable from *G. silus* in its absence of male breeding coloration, absence of sexual dimorphism wherein males are larger than females (the reverse condition is present), absence of notched zygosphenes and zygantra, and in the possession of an elongate (rather than truncated) and slender nasal process of the premaxilla. *Gambelia copei* is not easily diagnosed from *G. wislizenii,* as the primary character that supports the recognition of separate species is their narrowly overlapping distributions (see comments below). Additional differences include the absence of spotting on the head in all but one of 38 *G. copei* examined (SDSNH 18118, Bahia de San Francisquito, Baja California) and its darker dorsal coloration. Adjacent populations of *G. wislizenii* are easily diagnosed from *G. copei* as they are characterized by a pale dorsal coloration with numerous small punctations that are asymmetrically arranged, extend well onto the head, and continue well down onto the flanks.

Variation ($n = 21$).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by four to seven postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by six to seven internasals. Frontonasals occasionally enlarged. Canthals four; posterior one or two wider than high; seven to nine scales separate canthals of left and right sides. Supraorbital semicircles absent. Supraoculars small, flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals absent. Superciliaries eight to 12, extremely elongate medial scale present. Palpebrals ovoid, slightly convex, may be interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of four to seven rectangular scales, second, third, or fourth scale elongate. Supralabials 13 to 17, usually slightly longer than high except anteriormost scale, which is square. Lorilabials in two to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of postmentals that may be enlarged. Postmentals almost always separated from infralabials by sublabials on at least one side. Chinshields weakly differentiated or undifferentiated. Infralabials 12 to 17, square or wider than high, inferior border convex. Gulars usually flat, but occasionally convex and beadlike; each scale may be separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 160 to 200 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical in both sexes and all age groups. Paired, median row of subcaudals not larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 20 to 31, femoral pores extend beyond angle of knee, separated medially by ten to 18 granular scales. Subdigital lamellae on fourth toe 20 to 24.

Coloration in Life.—Individuals from southern San Diego County, the Sierra de Juarez and Sierra San Pedro Martir, and cismontane northwestern Baja California generally are dark brown in coloration with a pair of large paravertebral spots that are separated by broad, cream-colored transverse bars. There is much lateral flecking; however, lateral spots are lacking. Spots are nearly always absent from the head. In southern populations, such as those in the Vizcaino Desert, the base color of the dorsum is a paler golden tan, the dorsal spots are fragmented, and lateral spots may be present. In some southern individuals, the dorsal spotting may be nearly indistinguishable, with the dorsum peppered with fine pale speckling. This pattern may be more cryptic on the fine aeolian sand characteristic of the Vizcaino Desert (Grismer et al., 1994). The speckled pattern of the southern individuals appears to be an ontogenetic fragmentation of the color pattern characteristic of northern individuals as subadults have been examined with dorsal patterns very similar to those from the northern portion of the peninsula.

Gravid coloration in *G. copei* is similar to that of *G. wislizenii*, with orange or red spots often present on the head and/or neck, in two rows of spots on each flank, and on the ventral surface of the tail. Red or orange pigments may be present on the thighs as well. Males lack any form of breeding coloration.

A description of the dorsal pattern of *G. copei* (pattern C1) was provided in Montanucci (1978).

Size.—This species exhibits strong sexual dimorphism with females reaching larger adult size (maximum observed SVL = 126 mm) than males (maximum observed SVL = 120 mm).

Distribution (Fig. 50).—*Gambelia copei* occurs in extreme southcentral California in the vicinities of Cameron Corners (Mahrdt, 1973), Campo, and Potrero Grade southward through all but the San Felipe Desert region of northeastern Baja California to the northern portion of the cape region, Baja California Sur. The species is also found on the Pacific islands of Isla de Cedros, Isla Magdelena, and Isla Santa Margarita off of the west coast of the peninsula. *Gambelia copei* occurs in the lower Colorado Desert region between El Huerfanito and Bahia de San Luis Gonzaga and is also known from the gulf coast desert region in the vicinities of Bahia de Los Angeles and Punta San Francisquito. However, *G. copei* apparently does not inhabit the Gulf Coast desert region between Santa Rosalia and the vicinity of Loreto and may be excluded from this region by the intervening Sierra San Pedro and Sierra de La Giganta. This species occurs in high densities on the sandy plains of the Vizcaino Peninsula and its distribution appears to be limited to the western side of the peninsular ranges from this region to a point at least as far south as the southern terminus of the Sierra de La Giganta. It is known from as far south as 1 km N Rancho Tres Hermanos (N of Todos Santos) in the cape region of Baja California Sur.

The only published distribution map specific to *Gambelia copei* (Banta and Tanner, 1968) is flawed in a number of respects. First, the lower Colorado Desert region between San Felipe and Puertocitos is inhabited by *G. wislizenii* rather than *G. copei*. Second, *G. copei* is not known from the eastern half of the peninsula between Bahia de San Francisquito and La Paz. Finally, *G. copei* is not known to range throughout the cape region.

Gambelia copei is narrowly syntopic with *G. wislizenii* over a zone of approximately 1.6 km in Paseo de San Matias, Baja California (denoted by a rectangular mark on Figure 50). The two species are separated by a broad, transverse volcanic field that extends from the Sierra San Felipe to the gulf coast between Puertocitos and El Huerfanito, Baja California. This rugged volcanic flow, which is 31.5 km in width (by road), appears to act as an effective dispersal barrier for *Gambelia* along the gulf coast.

On the provided dot distribution map (Fig. 50), the question marks represent localities in Baja California Sur that are questionable because of imprecise locality data (CAS 18823—San Andreas [San Jorge]; MVZ 37260—Medano Blanco, 37262—sand dunes 12 mi SE Venancio).

Fossil Record.—None.

Natural History.—Very little has been written regarding the natural history of *Gambelia copei*, although it seems likely that it is similar to *G. wislizenii* in most aspects of its biology. This species is particularly common on the sparsely vegetated aeolian flats of the Vizcaino Peninsula, Baja California Sur, where it is often observed basking on roadside rocks, on the berms adjacent to graded dirt roads, or moving about in open spaces between clumps of vegetation. *Gambelia copei* is also found in more xeric creosote scrub habitats in the general vicinities of Paseo de San Matias, Bahia de San Luis Gonzaga, and Bahia de Los Angeles, Baja California, and in coastal sage scrub and oak woodland habitats on the western slopes of the Sierra San Pedro Martir and Sierra de Juarez (Welsh, 1988; personal observation). Where *G. copei* extends its range into extreme southcentral California, it apparently occurs in relatively densely vegetated chaparral.

Gambelia copei shares a number of behavioral similarities with *G. wislizenii* and *G. silus*. For example, all three share a habit of basking on small stones and roadsides berms. *Gambelia copei* also displays the familiar "freeze" behavior such that when they are threatened, they run to the base of a bush or thicket, flatten themselves to the ground, and remain motionless (Tevis, 1944; personal observation). Like *G. wislizenii*, this species appears to be a lizard predation specialist as evidenced by the presence of *Uta stansburiana* and *Callisaurus draconoides* in the stomach contents of museum specimens. Banta and Tanner (1968) observed a *Uta stansburiana* and a grasshopper in the stomach of an adult female (CAS 8843) from Isla de Cedros. Like its sister taxon *G. wislizenii*, females attain larger sizes than males. Although rigorous ecological data are lacking, *G. copei* appears to be nonterritorial as in *G. wislizenii* (personal observation).

Although little is known of the predators of *Gambelia copei*, they are likely to include the coachwhip snake (*Masticophis flagellum*) and patch-nosed snake (*Salvadora hexalepis*) as well as other saurophagous snake species, raptors, the Loggerhead Shrike (*Lanius ludovicianus*), the Greater Roadrunner (*Geococcyx californianus*), as well as a number carnivorous mammals such as the coyote (*Canis latrans*). Only one predation event has been observed by the author, in which a Loggerhead Shrike was observed carrying a nearly full-grown *G. copei*. The shrike could only fly short distances with the relatively large lizard and, when pursued, was forced to pin the dead lizard on the spine of a mesquite (*Prosopis*).

Adult *Gambelia copei* have been observed as early as 1 April 1993 in the vicinity of Cataviña, on 9 April 1993 on the Vizcaino Peninsula, and on 10 April 1992 in Paseo de San Matias, indicating that this species emerges from hibernation at a date similar to that of *G. wislizenii* from southern California (Miller and Stebbins, 1964; Tollestrup, 1979; Mitchell, 1984). Although adult females were observed in April, none were gravid, suggesting that reproductive activity had not yet commenced. The earliest that gravid females have been observed by the author is 3 May 1993 at the Paseo de San Matias locality. Gravid females have also been seen on 27 June 1991 in the Sierra San Borja and 4 July 1991 in the Sierra Santa Clara. An emaciated female that appeared to have recently deposited eggs also was observed on 4 July in the Sierra Santa Clara, indicating that mating probably took place in mid to late June. Fitch (1970) examined 90 leopard lizards from Baja California (but did not list localities, so it is possible that some of the specimens were *G. wislizenii*) and found two of two females collected in March to be gravid, as well as six of nine collected in June, and three of six collected in July. Thus, the reproductive season is more extensive than my observations would indicate.

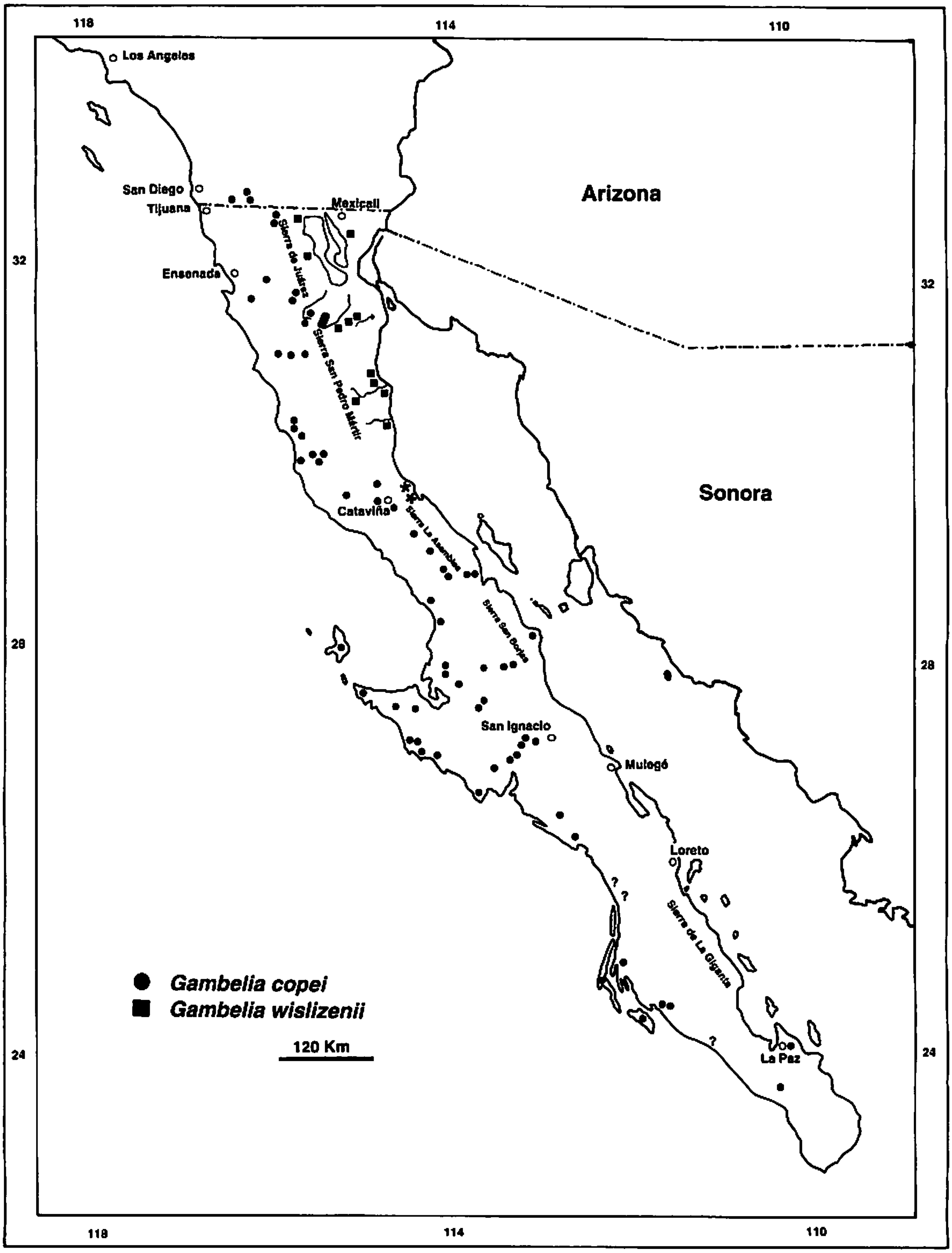

Fig. 50.—Geographic distribution of *Gambelia copei*. The small rectangular block in northern Baja California denotes the narrow zone where *G. copei* and *G. wislizenii* occur together. The asterisks represent sight records by the author for *G. copei* near Bahia de San Luis Gonzaga. The question marks along the Pacific coast of Baja California Sur indicate localities that must be considered questionable because of imprecise locality data.

Illustrations.—Black-and-white photographs of adult lizards were provided in Banta and Tanner (1968) and Montanucci (1978).

Taxonomic Remarks.-*Gambelia copei* and *G. wislizenii* are easily distinguished on the basis of their coloration (see diagnosis above). However, geographic variation in the dorsal coloration of *Gambelia wislizenii* is extensive and this alone is not particularly compelling evidence for the recognition of *copei* as a distinct species. The primary motivation for this taxonomic rearrangement is the occurrence of both forms in syntopy along a narrow zone within Paseo de San Matias in northeastern Baja California. Within Paseo de San Matias, individuals that are easily identified to species occur together in the same microhabitat over a zone of 1.6 km without showing any obvious evidence of intergradation. Aside from this narrow contact zone, the distributions of *G. copei* and *G. wislizenii* are widely separated.

Paseo de San Matias is a low elevation dispersal corridor that connects the lower Colorado Desert with the coastal region of northwestern Baja California. Several desert species extend their ranges westward toward the Pacific coast by way of this corridor and some coastal species nearly reach the desert by extending eastward (Welsh and Bury, 1984). It may appear as though *G. copei* and *G. wislizenii* are geographic variants and that the pattern change is the result of in situ selection where the habitat changes from extremely xeric creosote desert to more mesic mountainous terrain. However, typical *G. copei* occur in the lower Colorado Desert region in the vicinity of Bahia de San Luis Gonzaga, documenting that the distinctive color pattern of *G. copei* is not another *G. wislizenii* pattern type that appears only in mesic habitats. *Gambelia copei* in the Bahia de San Luis Gonzaga region are approached by *G. wislizenii* in the vicinity of Puertocitos, where they are separated by a transverse volcanic field that is 31.5 road km in width. This lava field extends from the peninsular ranges to the edge of the Gulf of California and appears to be a dispersal barrier for *Gambelia*. Because the color pattern differences noted above are maintained in these populations, which occur in essentially identical habitats that are separated only by the lava field, the notion that the *G. copei* and *G. wislizenii* color pattern differences are the result of in situ selection is unlikely. Nevertheless, because this taxonomic decision is based only on differences in coloration that are relatively subtle, on a single osteological character that differs in frequency (the presence of a well-developed tubercle on the anterolateral margin of the postorbital was present in all *G. copei* examined [$n = 8$], whereas in *G. wislizenii*, the tubercle usually is absent [present in four of 49 specimens]), and on presumed reproductive isolation in this region, the recognition of *G. copei* as a full species is considered tentative. Electrophoretic analyses of the Paseo de San Matias populations are planned in order to determine if fixed allelic differences can be detected that are consistent with the dorsal color pattern data.

Montanucci (1978) considered the populations of *Gambelia* on Isla Tiburon and coastal Sonora between Puerto Libertad and Bahia Kino to be con(sub)specific with *copei.* Although there are notable similarities between certain individuals from the coastal Sonoran region and those from Baja California (particularly in CAS 17050 from the southeastern end of Isla Tiburon), they differ in that the Sonoran lizards have spots that continue onto the dorsal surface of the head, whereas *G. copei* nearly always lack this spotting. While some individuals from coastal Sonora clearly resemble those of Baja California, the majority examined here were characteristic of those of the remaining portions of Sonora.

Gambelia corona† Norell

Gambelia corona Norell, 1989:11; fig. 10. Type locality: LACM locality 7058, Vallecito Badlands, Anza-Borrego Desert State Park (holotype: LACM 42880).

Etymology.—From the Latin *corona,* a crown, in reference to the distinctive characteristics of the frontal and frontoparietal suture.

Diagnosis.—*Gambelia corona*† is distinguished from other *Gambelia* by the presence of the frontoparietal suture anterior to the posterior extent of the orbits. It is further distinguished from *Gambelia copei* and *G. wislizenii* by the presence of a transversely concave frontal bone.

Distribution.—Known only from the type locality.

Remarks.—*Gambelia corona*† is an extinct species known only from a fossilized skull and mandibles. Black-and-white photographs of dorsal and lateral views of the skull were provided by Norell (1989).

Gambelia silus Stejneger

Crotaphytus silus Stejneger, 1890:105. Type locality: "Fresno, Cal." (holotype: USNM 11790A).
Crotaphytus wislizenii—Cope, 1900:255.

Gambelia wislizenii silus—Smith, 1946:164; pl. 31.
Crotaphytus (Gambelia) wislizeni silus—Weiner and Smith, 1965: 187.
Gambelia silus—Montanucci, Axtell, and Dessauer, 1975:339.
Gambelia sila—Jennings, 1987:11.

Etymology.—From the Latin *silus*, snub-nosed, in reference to the blunt snout of this species.

Diagnosis.—*Gambelia silus* is diagnosed from *G. corona*† by the presence of a frontoparietal suture that is posterior to the posterior border of the orbits. It is diagnosed from *G. wislizenii* and *G. copei* by the presence of territoriality, male breeding coloration, vertebrae with notched zygosphenes and zygantra, sexual dimorphism wherein males are larger than females, and in its truncated snout.

Variation (*n* = 15).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by six to eight postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by six to nine internasals. Frontonasals occasionally enlarged. Canthals four; posterior one or two wider than high; six to ten scales separate canthals of left and right sides. Supraorbital semicircles absent, although slightly enlarged scales corresponding to the supraorbital series occasionally evident. Supraoculars small, flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals absent. Superciliaries eight to 13, extremely elongate medial scale present. Palpebrals ovoid, slightly convex, may be interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of five to eight rectangular scales, second, third, or fourth scale elongate. Supralabials 13 to 16, usually slightly longer than high except anteriormost scale, which is square. Lorilabials in one to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately three to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of enlarged postmentals. Postmentals separated from infralabials by sublabials on at least one side. Chinshields weakly differentiated or undifferentiated. Infralabials 12 to 16, square or wider than high, inferior border convex. Gulars convex and beadlike; each scale separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 156 to 182 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical in both sexes and all age groups. Paired, median row of subcaudals not larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 15 to 20, femoral pores do not extend beyond angle of knee, separated medially by 17 to 25 granular scales. Subdigital lamellae on fourth toe 16 to 20.

Coloration in Life.—The dorsal base color ranges from pale tan, light or dark gray, or brown and the ventrum is white or yellowish. The dorsum is marked with seven to ten broad, pale transverse bars that may or may not be offsetting. Dark spots are often present between the pale crossbars and generally extend onto the temporal region of the head. The crossbars occasionally may be fragmented into light spots and a vertebral stripe may be present (Montanucci, 1965). Spots and crossbars similar to those of the back are generally present on the limbs and tail, although the crossbars may be absent from the forelimbs. The tail becomes banded distally as described in the generic account.

The posterior of the thigh and the underside of the tail in juveniles is suffused with yellow pigments. Males in certain parts of the range (particularly the foothills surrounding the San Joaquin valley) develop a breeding color composed of either a bright rusty red suffusion of the abdomen and the ventral and dorsal surfaces of the hindlimbs and tail or a bright salmon color that extends over the entire ventral surface of the body and limbs, sometimes including the gular region as well (Montanucci, 1965). Occasionally, individuals may develop this coloration only laterally (Montanucci, 1970). Gravid coloration in this species is similar to that of *G. copei* and *G. wislizenii* in that the orange or red pigments are deposited on the lateral surfaces of the head and flanks, on the under surface of the tail, and occasionally on the thighs. However, this pattern differs from that of *G. copei* and *G. wislizenii* in that the pigments are generally deposited in a single row along each flank, rather than in two rows (Montanucci, 1970).

The dorsal pattern of *Gambelia silus* was described more fully in Van Denburgh (1922), Smith (1946), and Montanucci (1965, 1970).

Size.—This species exhibits strong sexual dimorphism with males reaching larger adult size (maximum observed SVL = 120 mm) than females (maximum observed SVL = 111 mm; Tollestrup, 1979, 1982).

Distribution (Fig. 51).—*Gambelia silus* is restricted to the San Joaquin valley of California and its surrounding foothills. They range between "the old town of Carnegie in Corral Hollow," San Joaquin County, in the north to the Cuyama Valley and base of the Tehachapi Mountains in the south. The species apparently does not contact *G. wislizenii* presently, although Montanucci (1970) identified an isolated population of putative hybrid origin between the two species in the Cuyama River drainage system southwest of the southern end of the San Joaquin valley. Although *G. silus* and *G. wislizenii* are isolated from one another, *Gambelia wislizenii* approaches *G. silus* in the Cuyama valley drainage where *G. wislizenii* occurs above 1100 m and *G. silus* occurs below 790 m (Montanucci, 1970).

Fossil Record.—No fossil specimens have been referred to this species, although Brattstrom (1953) considered measurements of two maxillae taken from McKittrick, Kern County, California, a locality within the current distributional confines of *Gambelia silus,* to conform more closely to extant *G. wislizenii* than to *G. silus.* However, examination of his figures renders this observation suspect as neither fossil has a complete nasal process. On distributional grounds, it would appear more likely that these specimens represent *G. silus.* Because the material has not been reexamined here, the reference to *G. wislizenii* is considered questionable.

Natural History.—Montanucci (1965, 1967, 1970) and Tollestrup (1979, 1982, 1983) studied the ecology of *Gambelia silus* and all of the comments provided here are taken from these references unless otherwise noted. According to Montanucci (1965), the species inhabits sparsely vegetated plains, alkali flats, low foothills, canyon floors, large washes, and arroyos. They prefer open habitat and are absent or rare in areas with dense vegetation or tall grass. As is the case with *G. wislizenii,* the species appears to be most common in areas with abundant rodent burrows. Common vegetational associates include grasses (*Stipa*), saltbush (*Atriplex*), and iodinebush (*Allenrolfea occidentalis*).

In contrast with *Gambelia wislizenii* (and presumably *G. copei*), *G. silus* is highly territorial and males from many, but not all, populations develop rusty red coloration during the breeding season (Montanucci, 1965; Tollestrup, 1979, 1982). The activity season commences in late March or early April and extends through late September, although some juveniles may remain active into October given favorable weather conditions (Montanucci, 1965; Tollestrup, 1979). The mating season occurs primarily in late April and May, although Germano and Williams (1992) observed gravid females as late as mid-July, and young hatch in late July or early August (Montanucci, 1965; Tollestrup, 1979, 1983). Clutch size is smaller than that of *G. wislizenii,* with a range of two to six and a mean of 2.90 (Tollestrup, 1979, 1982) to 3.30 (Montanucci, 1970). Germano and Williams (1992) documented that as many as four clutches may be deposited per reproductive season.

Gambelia silus shares a number of behavioral similarities with *G. copei* and *G. wislizenii.* All three are often observed basking on small roadside rocks and the berms along the edges of graded dirt roads. "Freeze" behavior (Montanucci, 1965), wherein threatened individuals run to the base of a nearby bush, flatten themselves to the ground, and remain motionless (presumably as a means of avoiding detection) is also a shared behavior.

Montanucci (1965) indicated that *Gambelia silus* feeds primarily upon locusts (Orthoptera), cicadas (Homoptera), and small lizards, including *Uta stansburiana, Phrynosoma coronatum, Cnemidophorus tigris,* and *Sceloporus magister.* Germano and Williams (1994) observed that *G. silus* eat young conspecifics, as well. Tollestrup (1979) found no evidence of lizard predation at her southern San Joaquin valley study sites and noted the following arthropod prey items: orthopterans, coleopterans, hymenopterans, dipterans, homopterans, lepidopterans, and spiders. Regional or seasonal variation may explain the discrepancies in food preferences found in these studies.

Montanucci (1965) noted predation on *Gambelia silus* by several avian species including Loggerhead Shrikes (*Lanius ludovicianus*), American Kestrels (*Falco sparverius*), Burrowing Owls (*Athene cunicularia*), and Greater Roadrunners (*Geococcyx californianus*). Prarie Falcons (*Falco mexicanus*) are also known to capture this species (Germano and Carter, 1995). Montanucci (1965) also observed predation by the coachwhip snake (*Masticophis flagellum*) and the gopher snake (*Pituophis melanoleucus*). Other potential predators include the spotted skunk (*Spilogale putorius*) and the ground squirrel (*Spermophilus beecheyi*), both of which consumed *G. silus* when captured together in barrel traps, as well as the coyote (*Canis latrans*), badger (*Taxidea taxus*), glossy snake (*Arizona elegans*), long-

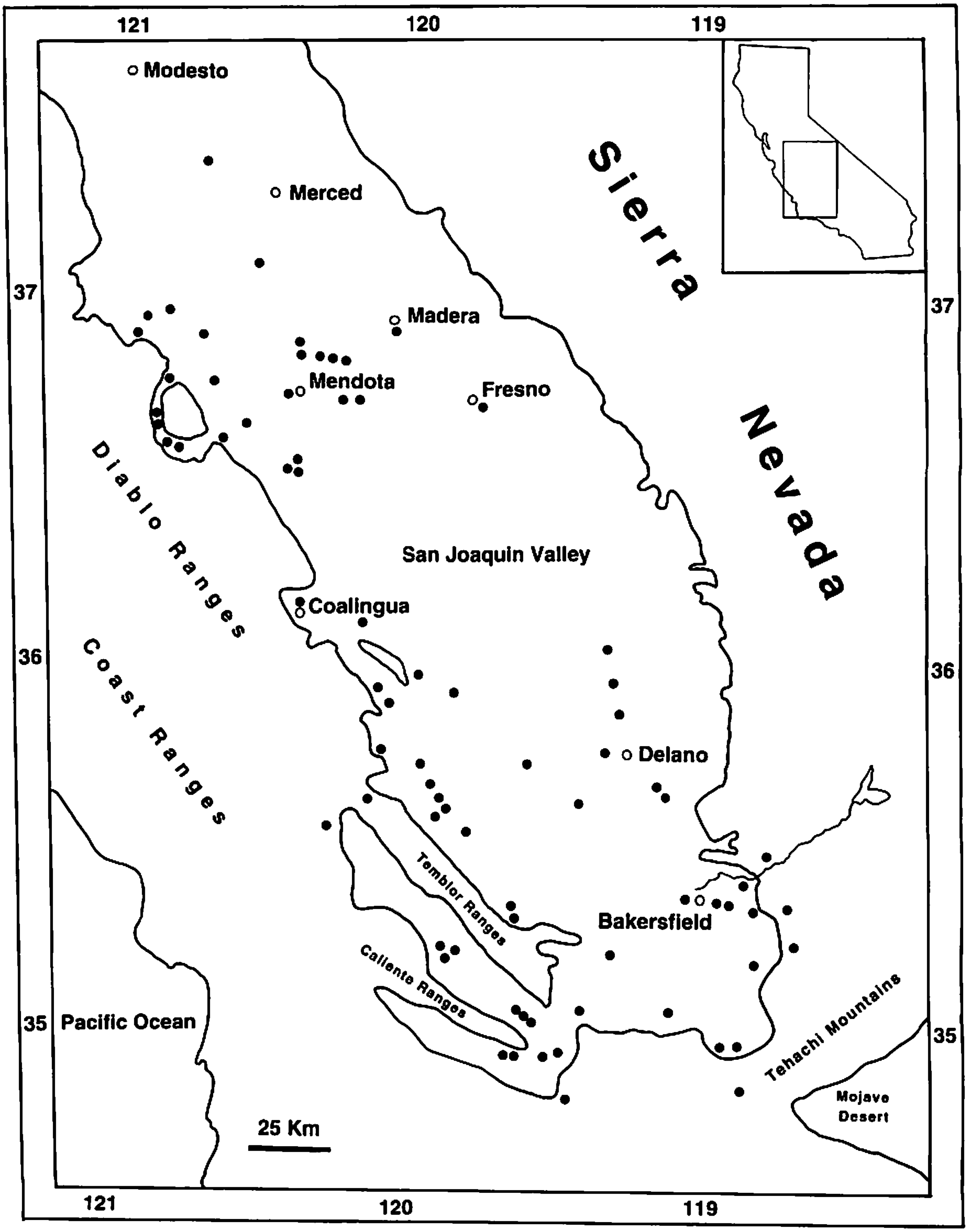

Fig. 51.—Geographic distribution of *Gambelia silus.*

nosed snake (*Rhinocheilus lecontei*), and common kingsnake (*Lampropeltis getula*).

Remarks.—*Gambelia silus* is now extinct over much of it historical range due primarily to habitat degradation associated with agricultural development of the San Joaquin valley. As of 1990, only seven percent of the San Joaquin valley had not been altered by agricultural and urban development

(Steinhart, 1990). As a result, this species is a federally and state listed endangered species.

Illustrations.—Montanucci (1965) provided a line drawing of the snout squamation; black-and-white photographs were provided by Van Denburgh (1922), Smith (1946), and Pickwell (1972); color illustrations were given in Smith and Brodie (1982) and Stebbins (1985); color photographs were provided in Behler and King (1979) and Steinhart (1990).

Gambelia wislizenii Baird and Girard
(Fig. 30A)

Crotaphytus wislizenii Baird and Girard, 1852:69. Type locality: "near Santa Fe," New Mexico (holotype: USNM, now lost or destroyed); invalid holotype (Yarrow 1882*a*): USNM 2770; invalid lectotype (Tanner and Banta 1963): USNM 2685.

Crotaphytus gambelii Baird and Girard (syn. fide Cope, 1900), 1852:126. Type locality: "Not precisely known. . .California" (holotype: USNM 2722).

Crotaphytus fasciatus Hallowell (syn. fide Cope, 1900), 1852:207. Type locality: "Sand hills, at the lower end of the Jornada del Muerte, New Mexico" (holotype: USNM 2736).

Leios. [*aurus*] *fasciatus*—Duméril, 1856:533.

L. [*eiosaurus*] *hallowellii* Duméril (substitute name for *L. fasciatus* Hallowell, 1852), 1856:533.

Crotaphytus (*Gambelia*) *wislizenii*—Baird, 1858:253.

Gambelia wislizenii—Smith, 1946:158; fig. 57, 68; pl. 30.

Crotaphytus (*Gambelia*) *wislizeni punctatus* Tanner and Banta, 1963:138; fig. 1–5. Type locality: "Yellow Cat Mining District approximately 10 miles south of U.S. Highway 50–6, Grand County, Utah" (holotype: BYU 20928).

Crotaphytus (*Gambelia*) *wislizeni*—Weiner and Smith, 1965:186; fig. 1–6.

Crotaphytus wislizenii neseotes—Banta and Tanner (syn. fide Montanucci, 1978), 1968:186; fig. 1–5. Type locality: "Cedros Island; west coast of Baja California Norte, Mexico" (holotype: CAS 79872).

Gambelia wislizeni—Montanucci, Axtell, and Dessauer, 1975: 339.

Crotaphytus wislizeni maculosus—Tanner and Banta, 1977:230; fig. 2–4. Type locality: "approximately 200m W of the lookout point along Nevada Highway 33, west side of Pyramid Lake, Washoe County, Nevada" (holotype: BYU 32685).

Etymology.—Named in honor of Dr. Frederick Adolphus Wislizenus, an army surgeon, who collected the original type specimen.

Diagnosis.—*Gambelia wislizenii* is distinguished from *G. corona*† by the absence of a broad, transversely concave frontal bone, the presence of a frontoparietal suture posterior to the posterior extent of the orbits, and an elongate and slender nasal process of the premaxilla. It is diagnosable from *G. silus* in its absence of male breeding coloration, absence of sexual dimorphism wherein males are larger than females (the reverse condition is present), absence of notched zygosphenes and zygantra, and in the possession of an elongate (rather than truncated) and slender nasal process of the premaxilla. For a diagnosis distinguishing *G. wislizenii* and *G. copei*, see discussion under the *G. copei* taxonomic account.

Variation (*n* = 20).—Rostral approximately four times wider than high, usually rectangular in shape. Rostral bordered by five to eight postrostrals. Remaining snout scales irregularly arranged, an enlarged middorsal series may be present. Nasals separated by six to nine internasals. Frontonasals occasionally enlarged. Canthals four; posterior one or two wider than high; seven to nine scales separate canthals of left and right sides. Supraorbital semicircles absent. Supraoculars small, flat or convex, smooth, becoming progressively larger medially such that medial scales are two to four times larger than lateral ones. Circumorbitals absent. Superciliaries seven to 13, extremely elongate medial scale present. Palpebrals ovoid, slightly convex, may be interspersed with numerous interstitial granules. Preoculars, suboculars, and postoculars form an arc of four to seven rectangular scales, second, third, or fourth scale elongate. Supralabials 12 to 17, usually slightly longer than high except anteriormost scale, which is square. Lorilabials in one to four rows, ovoid to rectangular, juxtaposed, separating supralabials from suboculars and nasals. Aperture of external auditory meatus rectangular or ovoid, often constricted at or above the midpoint, approximately two to four times higher than wide, with small, strongly convex, somewhat conical auricular scales lining anterior margin. Mental pentagonal, one to 1.5 times wider than high, bordered laterally by anterior infralabials and posteriorly by a pair of postmentals that may be enlarged. Postmentals almost always separated from infralabials by sublabials on at least one side. Chinshields weakly differentiated or undifferentiated. Infralabials 12 to 17, square or wider than high, inferior border convex. Gulars usually flat, but occasionally convex and beadlike (especially in southern portion of range); each scale may be separated from adjacent scales by numerous asymmetrically arranged interstitial granules.

Dorsal scales in approximately 158 to 224 rows midway between forelimb and hindlimb insertions. Tail long, cylindrical in both sexes and all age groups. Paired, median row of subcaudals not larger than adjacent subcaudals and lateral caudals. Enlarged postanal scales present in males.

Deep postfemoral dermal mite pocket present at hindlimb insertion. Femoral pores 15 to 25, femoral pores extend beyond angle of knee, separated medially by 14 to 25 granular scales. Subdigital lamellae on fourth toe 18 to 25.

Coloration in Life.—The dorsal pattern of *G. wislizenii* is extremely variable, with several color morphs that are more or less confined to specific geographic regions. These pattern classes conform to the subspecies *wislizenii, punctatus,* and *maculosus* (Montanucci, 1978; although he recognized an additional unnamed pattern class as well) that are not recognized here. They differ most notably in the size of the dorsal spots (large in the *maculosus* pattern class, intermediate in *wislizenii,* and small in *punctatus*), as well as in the character of the dorsal transverse bars. The dorsal spots are often scattered over the dorsum irregularly, extend well down onto the flanks, and continue onto the dorsal and lateral surfaces of the head. The dorsal base color for most individuals is white, cream, or gray, although some individuals apparently may approach the brown coloration of northern *G. copei* (Montanucci, 1978).

Gravid coloration in *G. wislizenii* is similar to that of *G. copei* with orange or red spots often present on the head and/or neck, in two rows of spots on each flank, and on the ventral surface of the tail. The red or orange pigments occasionally may extend onto the thighs. Males lack any form of breeding coloration.

A more detailed description of geographic variation in the dorsal pattern of *Gambelia wislizenii* is provided in Montanucci (1978).

Size.—This species exhibits strong sexual dimorphism with females reaching larger adult size (maximum observed SVL = 144 mm) than males (maximum observed SVL = 119 mm; Tollestrup, 1979, 1982).

Distribution (Fig. 52).—*Gambelia wislizenii* occurs in the western United States and northern Mexico, ranging from eastern Oregon and southern Idaho in the north, at least as far south as central Sonora in the west, and southern Coahuila or northern Zacatecas in the east. This species extends westward well beyond the limits of the lower Colorado Desert in southern California where it has been collected at Temecula, near Vail Lake, and at Arlington in Riverside County. However, a specimen purportedly collected at Arcadia, Los Angeles County (FMNH 203919), seems suspect. The species appears to be absent from the high elevation mountains of eastern Arizona and adjacent western New Mexico. Its distribution also appears to be limited in Texas, with a number of specimens known from the sandy northern portion of the Texas panhandle and from the Chihuahuan Desert habitats between Big Bend National Park and El Paso. It is unclear whether *G. wislizenii* is continuously distributed in the western portion of Texas between Reeves, Ward, and Crane counties and the southern portions of Brewster and Presidio counties. Specimens are relatively few from most of northern Mexico, but it appears that *G. wislizenii* is completely excluded from the higher portions of the Sierra Madre Occidental of eastern Sonora and western Chihuahua. *Gambelia wislizenii* and *G. copei* occur together in a narrow zone of syntopy in northern Baja California which is denoted in Figure 52 by an oblong oval marking (for a more extensive discussion of this zone of syntopy, see the *G. copei* account above). The two northern Oregon localities shown on Figure 52 are old records from The Dalles, Wasco County, and Hat Rock, Umatillo County. The symbol "?" shown on Figure 52 represents a record from Cheney, Spokane County, Washington. The northern Oregon and Washington records should be considered questionable until verified by additional field work.

Fossil Record.—Numerous Pleistocene fossils have been referred to this species (Estes, 1983) including a pair of maxillae that may be more properly referred to *Gambelia silus* (see *G. silus* account for comments).

Natural History.—There is extensive literature associated with the natural history and ecology of *Gambelia wislizenii.* The reader is referred to the following papers for a more detailed discussion of this topic: McCoy, 1967; Montanucci, 1967, 1970, 1978; Turner et al., 1969; Tanner and Krogh, 1974*a*, 1974*b*; Essghaier and Johnson, 1975; Parker and Pianka, 1976; Tollestrup, 1979, 1982, 1983; and Mitchell, 1984. This widespread species occurs in a number of habitat types, although it is found primarily on desert flats and lower foothills characterized by sparse vegetation. Throughout much of its range in the Sonoran, Mojave, Great Basin, and Chihuahuan deserts it is found in flatlands in association with creosote bush (*Larrea tridentata*) as well as other xerophilic plants. In the Pyramid Lake region of northwestern Nevada, it is found in association with filaree storksbill (*Erodium cicutarium*), mormon tea (*Ephedra nevadensis*), four-wing saltbush (*Atriplex canescens*), and *Grayia spinosa* (Snyder, 1972). Tollestrup (1979, 1982, 1983) studied *G. wislizenii* near California City, California, where the dominant shrub was creosote bush (*Lar-*

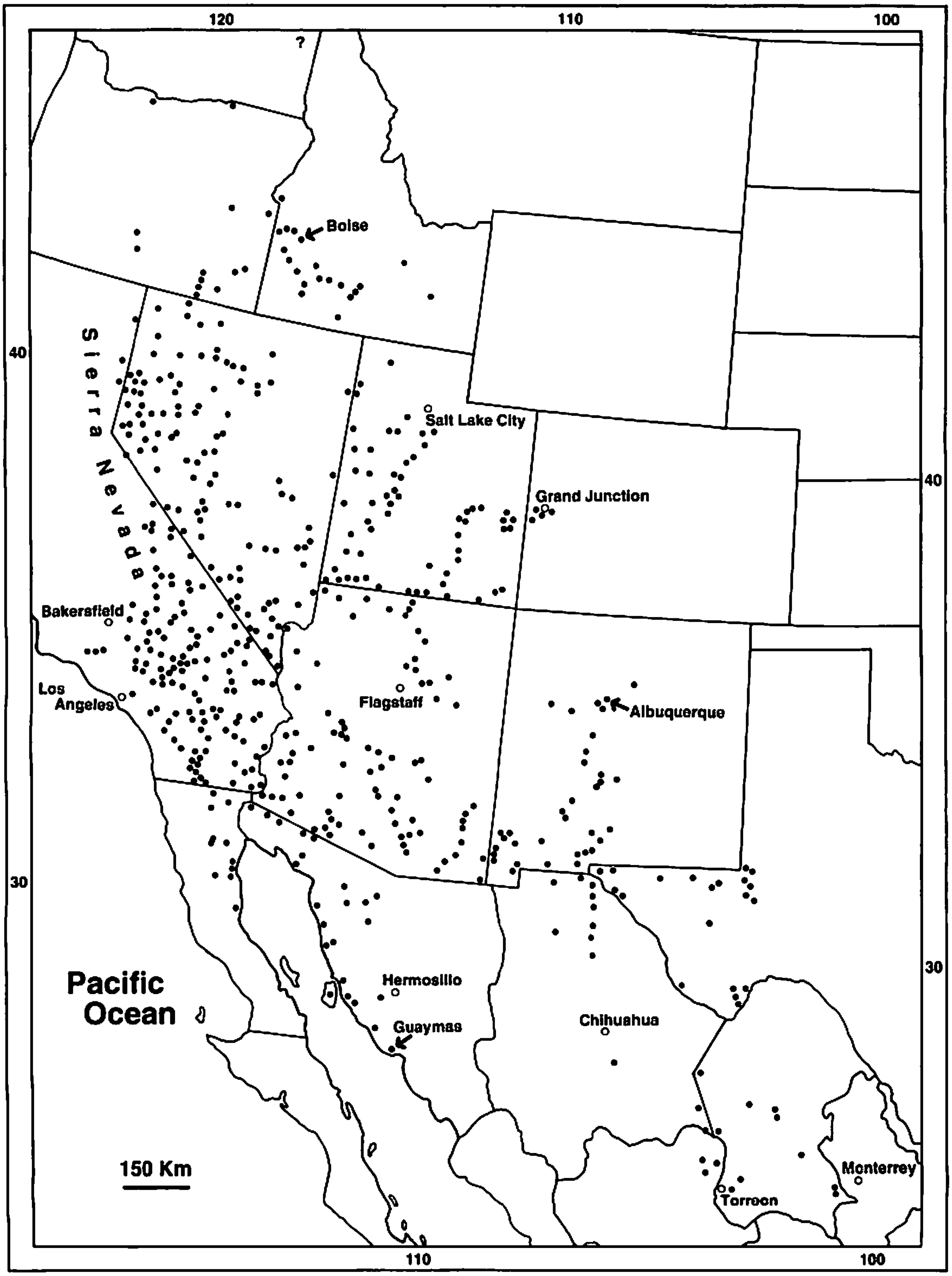

Fig. 52.—Geographic distribution of *Gambelia wislizenii.* The elongate ovoid marking in northern Baja California represents the narrow zone in which *G. wislizenii* and *G. copei* occur together. The "?" denotes a questionable locality record from Cheney, Spokane County, Washington.

rea tridentata), and other major components of the vegetation included saltbush (*Atriplex*), *Haplopappus*, *Lycium andersonii*, and *Dalea*. McCoy (1967) discussed the ecology of this species in the Colorado River valley, Mesa County, Colorado, where it was found in association with greasewood (*Sarcobatus vermiculatus*) and big sage (*Artemisia tridentata*). In southeastern Arizona, the species was found on sand dunes with sand sage (*Artemisia filifolia*) and indigo bush (*Dalea* sp.) and on bajadas characterized by cat-claw acacia (*Acacia constricta*), jimmyweed (*Haplopappus taenuisecta*), *Opuntia*, and *Agave* (Mitchell, 1984). Near the northeastern limits of its range (11.5 mi S Monahans, Ward County, Texas), Tinkle (1959) found them on sandy flatlands in association with mesquite (*Prosopis*), creosote bush (*Larrea tridentata*), *Acacia*, and dwarf shin oak (*Quercus havardii*). Montanucci (1970) found *G. wislizenii* restricted to the high elevation (above 3600 ft) pinyon–juniper woodland habitats of the Cuyama and Lockwood valleys, southern California, near the hybrid zone between this species and *G. silus*. However, the pinyon–juniper zone is thought to be suboptimal habitat for *G. wislizenii* and they are often absent from such areas (Tanner and Jorgenson, 1963; McCoy, 1967). *Gambelia wislizenii* appears to be most common on sparsely vegetated flatlands with large numbers of rodent burrows (Tanner and Banta, 1963; McCoy, 1967; Nussbaum et al., 1983).

Unlike *Crotaphytus* and *Gambelia silus*, *G. wislizenii* lacks territoriality (McCoy, 1967; Montanucci, 1970; Tollestrup, 1979, 1982, 1983) and there is often much overlap in home ranges (Tollestrup, 1979, 1983). Females may even nest communally (Parker and Pianka, 1976). Females attain much larger size than males and appear to consume a higher proportion of vertebrate prey (Parker and Pianka, 1976; Tollestrup, 1979, 1982, 1983). Southern populations reach larger adult sizes than more northern populations which Parker and Pianka (1976) again linked to an increased emphasis on vertebrate prey. *Gambelia wislizenii* are ambush predators, often resting in the shadows at the base of a bush before dashing out to capture passing prey items (Tollestrup, 1979, 1983). They are able to move with great speed and have been observed to leap as high as 0.6 m to capture flying insects (Franklin, 1914). Known prey items include arthropods, especially orthopterans, as well as coleopterans, lepidopterans, hymenopterans, hemipterans, homopterans, dipterans, isopterans, neuropterans, and arachnids (Knowlton and Thomas, 1936; McCoy, 1967; Snyder, 1972; Tanner and Krogh, 1974*a*, 1974*b*; Essghaier and Johnson, 1975; Parker and Pianka, 1976; Tollestrup, 1979; Mitchell, 1984). Vertebrate prey include the lizards *Callisaurus draconoides*, *Cnemidophorus tessellatus*, *C. tigris*, *Uta stansburiana*, *Phrynosoma platyrhinos*, *Sceloporus graciosus*, *S. undulatus*, smaller *G. wislizenii*, and small snakes, as well as the pocket mouse *Perognathus longimembris* (Taylor, 1912; Richardson, 1915; Camp, 1916; Van Denburgh, 1922; Knowlton and Thomas, 1936; Banta, 1967; McCoy, 1967; Snyder, 1972; Tanner and Krogh, 1974*a*, 1974*b*; Parker and Pianka, 1976; Tollestrup, 1979, 1983; Pietruszka et al., 1981; Crowley and Pietruszka, 1983). As has been reported for several *Crotaphytus* species (i.e., *C. bicinctores*, *C. vestigium*), *Lycium* berries are often consumed and may even represent a preferred food item during parts of June and July (Tanner and Krogh, 1974*a*). Turner et al. (1969) observed individuals climbing into *Lycium* bushes to eat the berries, indicating that this plant material is not consumed inadvertently. Jorgensen and Orton (1962) collected two *G. wislizenii* in traps baited with oatmeal and found oatmeal in the stomach contents of both.

Gambelia wislizenii shares a number of behavioral similarities with *G. copei* and *G. silus*. All three are often observed basking on small roadside rocks and the berms along the edges of graded dirt roads. "Freeze" behavior (Brooking, 1934; McCoy, 1967) wherein threatened individuals run to the base of a nearby bush, flatten themselves to the ground, and remain motionless (presumably as a means of avoiding detection) is also a shared behavior. A behavior present in *G. wislizenii* but not yet noted in other *Gambelia* is vocalization (Taylor, 1912; Jorgensen et al., 1963; Wever et al., 1966; Crowley and Pietruszka, 1983). Wever et al. (1966) described the sound emitted as "vocal cries of a wailing or moaning character." The ability to vocalize, although extremely unusual within iguanians, has also been noted in *C. bicinctores* (Smith, 1974) suggesting that all crotaphytids may possess this ability.

Accounts of predation on *Gambelia wislizenii* are rare in the literature. Tollestrup (1979) observed a failed predation attempt on an adult female by a Prairie Falcon (*Falco mexicanus*). Tollestrup (1979) considered the following species to be potential predators at the California City study site: the coachwhip snake (*Masticophis flagellum*), sidewinder

(*Crotalus cerastes*), Mojave rattlesnake (*Crotalus scutulatus*), Loggerhead Shrike (*Lanius ludovicianus*), raptors, Burrowing Owl (*Speotyto cunicularia*), badger (*Taxidea taxus*), coyote (*Canis latrans*), and kit fox (*Vulpes macrotis*). To this list can be added *G. wislizenii*, which commonly preys on smaller individuals of its own species and a number of saurophagous snakes that occur within its range, such as the patch-nosed snake (*Salvadora* sp.), the common kingsnake (*Lampropeltus getula*), the gopher snake (*Pituophis melanoleucus*), the glossy snake (*Arizona elegans*), and the long-nosed snake (*Rhinocheilus lecontei*).

The length of the activity season of *Gambelia wislizenii* varies latitudinally. Northern and northeastern populations (western Colorado, Utah, northwestern Nevada, and Ward County, Texas) may not emerge from hibernation until early or even late May (Tinkle, 1959; McCoy, 1967; Snyder, 1972; Parker and Pianka, 1976). Adults enter hibernation in early August and, thus, may have activity seasons less than three months in length (McCoy, 1967). Individuals from southern populations emerge from hibernation in late March or early April (southeastern Arizona, vicinity of California City, Joshua Tree National Monument) and enter hibernation in late August to late October (Miller and Stebbins, 1964; Tollestrup, 1979; Mitchell, 1984). Reproduction appears to be concentrated in late May and early June in the California City and southeastern Arizona populations and after these dates gravid females were not observed (Tollestrup, 1979, 1982; Mitchell, 1984). In Utah and western Colorado, gravid females were observed between early June and early July, indicating that the reproductive season is pushed back by a few weeks in more northern populations (McCoy, 1967; Parker and Pianka, 1976). Clutch size also varies from population to population, with mean clutch sizes ranging between 5.15 (Robison and Tanner, 1962) and 7.3 (McCoy, 1967; Mitchell, 1984). Most studies have found no evidence of multiple clutch production (McCoy, 1967; Tanner and Krogh, 1974*a*; Parker and Pianka, 1976; Tollestrup, 1979, 1982; Mitchell, 1984), although Turner et al. (1969) observed second clutches in a southern Nevada population.

Gambelia wislizenii develop vibrant orange or reddish gravid coloration shortly before ovulation (as do all crotaphytid species). This coloration is maintained throughout the gravid period and is lost soon after parturition. The fecal matter of females that are losing their gravid coloration may be heavily saturated with similar orange pigments and this may provide a clue to the yet-to-be-identified pigment type responsible for this coloration.

Illustrations.—Numerous photographs and illustrations have been published. Detailed black-and-white illustrations of the entire animal were provided by Baird and Girard (1852*c*), Hallowell (1852), Baird (1859), and Stebbins (1954); ventral head squamation (Stebbins, 1954); head, limb, and preanal squamation by Cope (1900); skull, pelvic and pectoral girdles by Weiner and Smith (1965); anterior body and head musculature by Robison and Tanner (1962); black-and-white photos were presented by Van Denburgh (1922), Tanner and Banta (1963, 1977), Pickwell (1972), Montanucci (1978), and Nussbaum et al. (1983); color illustrations by Stebbins (1985) and Conant and Collins (1991); colorized photo by Ditmars (1920); color photographs were provided by Leviton (1971), Behler and King (1979), Hammerson (1986), and Garrett and Barker (1987).

Taxonomic Remarks.—The subspecies *Gambelia wislizenii punctatus* and *G. w. maculosus* often are considered to be synonyms of *G. w. wislizenii* and in their descriptions, broad intergrade zones were identified (Tanner and Banta, 1963, 1977). Furthermore, Montanucci (1978) showed that the *G. w. maculosus*, *G. w. punctatus*, and *G. w. wislizenii* dorsal pattern classes occur sporadically throughout the range of *G. wislizenii*. Based on these data, *G. w. maculosus* and *G. w. punctatus* are here considered to be pattern classes and are synonymized with *G. wislizenii*.

No official holotype specimen of *Crotaphytus wislizenii* was designated by Baird and Girard (1852*a*) and this created some confusion when later workers attempted to rectify the situation. Tanner and Banta (1963) designated a lectotype (which they referred to as a holotype) for *C. wislizeni* after recognizing that Yarrow (1882*a*) had incorrectly designated USNM 2770 as the type specimen, and that the original specimen figured by Baird and Girard (1852*c*) from near Santa Fe, New Mexico, had been lost or destroyed. The specimen of *Crotaphytus wislizenii* (USNM 2770) designated by Yarrow (1882*a*) was collected by H. Baldwin Möllhausen in Colorado probably in 1853–1854 after *C. wislizenii* had already been described (Tanner and Banta, 1963) and therefore could not have represented the original type specimen described by Baird and Girard (1852*a*). The designation of a lectotype requires that the original description of the species was based on a series of syntypes, rather than a single holotype. In their description, Baird and Girard (1852*a*) stated: "Head proportionally narrow and elongated; cephalic plates and scales on the back very small: yellowish brown, spotted all over with small patches of deeper brown or black. Caught near Santa Fé, by Dr. Wislizenius (sic); specimens of the same species sent in by Lieut. Col. J. D. Graham, collected between San Antonio and El Paso del Norte." Thus, the description of the species appears to be based on the specimen from near Santa Fe, whereas the other specimens were referred to the species afterward. Therefore, according to the International Commission of Zoological Nomenclature (1985), it is inappropriate to designate a lectotype for the species. Furthermore, except under "exceptional circumstances," a neotype is not to be designated either. "Exceptional circumstances," such as when a neotype is necessary in the interests of stability of nomenclature, clearly are not evident at present. Therefore, USNM 2685 (collected between San Antonio and El Paso del Norte), which was designated as the lectotype by Tanner and Banta (1963), should not be recognized as either a lectotype or a neotype. If the designation of a neotype should become necessary, it should be collected in the immediate vicinity of Santa Fe, New Mexico.

KEY TO THE SPECIES OF *CROTAPHYTUS* AND *GAMBELIA*

A key to the species of *Crotaphytus* is not difficult to produce for adult males because most species are easily distinguished on the basis of conspicuous color pattern characteristics. A key for adult females and juveniles of both sexes is more difficult because many of the characteristics that distinguish species are present only in adult males. Adult male *Crotaphytus* are easily distinguished from females by the presence of conspicuous gular coloration, larger femoral pores with a greater quantity of exudate, and often by the presence of enlarged postanal scales. A number of additional sexually dichromatic features may also be employed depending on the species in question (see taxonomic accounts). With regard to *Gambelia*, the formulation of a key is difficult for both sexes and all age classes due to variation in the coloration of *G. wislizenii* and *G. silus* and the absence of distinctive features of squamation. With a few notable exceptions, all species of *Crotaphytus* and *Gambelia* are allopatrically distributed with respect to their congeners. Thus, geography is usually a reliable means for determining species identifications when morphology fails. Fortunately, where geographic overlap occurs, the species in question are easily distinguished. Note: The key to juvenile *Crotaphytus* does not include *C. antiquus* for which no specimens are available.

Key to the Species of *Crotaphytus*
(Adult Males)

1\. Dorsal pattern comprised of white or pale gray net-like reticulations on a golden tan or brown dorsal base color, femoral pores jet black (Fig. 30C, D) 2

1a. Dorsal pattern composed of white spots and/or dashes, with or without white transverse bars, on a brown, blue, green, tan, or straw yellow dorsal base color; femoral pores off-white or gray (Fig. 31, 32) 3

2\. Dorsal coloration golden tan, groin patches absent (Fig. 30C, 33) .... *reticulatus*

2a. Dorsal coloration brown, groin patches present (Fig. 30D) .... *antiquus*

3\. Anterior collar markings incomplete ventrally (do not pass through the gular fold (Fig. 33) .... *collaris*

3a. Anterior collar markings complete ventrally (Fig. 34, 35) 4

4\. Tail round or nearly so in cross section without an off-white vertebral stripe; small melanic inguinal patches are present but confined to immediate vicinity of groin (Fig. 31A, 34) .... *nebrius*

4a. Tail strongly compressed laterally with a white or off-white vertebral stripe; large melanic inguinal patches extend half way to the forelimb insertion or more (Fig. 31B, 32A–D, 35) 5

5\. Dorsal coloration aquamarine to cobalt blue; black oral melanin present (Fig. 31B) .... *dickersonae*

5a. Dorsal coloration dark brown; black oral melanin absent (Fig. 32A–D) 6

6\. Posterior collar markings absent or extremely reduced; white component of dorsal pattern composed of irregularly arranged, elongate, wavy white lines (Fig. 32D) .... *insularis*

6a. Posterior collar markings present; white component of dorsal pattern composed of white spots and/or dashes, with or without regularly arranged white transverse bars (Fig. 31A–C; 32A, B) 7

7\. White dorsal transverse bars present (Fig. 32C); olive green or yellow-orange ventrolateral breeding coloration present; posterior collar markings widely separated dorsally .... *vestigium*

7a. White dorsal transverse bars absent, olive green or yellow-orange ventrolateral breeding coloration absent; posterior collar markings in contact or narrowly separated dorsally 8

8\. Granular ventrolateral reticulations present; pale orange or peach-colored transverse bands incorporated into brown dorsal base coloration; white bar that separates anterior and posterior collar markings lacks green tint; hindlimb brown with a white or off-white reticulate pattern over entire dorsal surface .... *bicinctores*

8a. Granular ventrolateral reticulations absent; white bar that separates the anterior and posterior collar markings with a pale green tint; hindlimb spotted proximally but patternless from just above the knee to the distal terminus .... *grismeri*

Key to the Species of *Crotaphytus* (Adult Females)

1. Dorsal pattern comprised of white or pale gray net-like reticulations, at least some of which surround gray or black pigments, on a golden tan or brown dorsal base color 2

1a. Dorsal pattern composed of white spots and/or dashes, with or without white transverse bars, on a pale brown, bluish, greenish, tan, or straw yellow dorsal base color (Fig. 31C) 3

2. Postfemoral mite pockets absent; at least three of the scales of the right and left supraorbital semicircles in contact .... *reticulatus*

2a. Postfemoral mite pockets present; supraorbital semicircles either separated by a continuous row of scales or with one or rarely two scales of the supraorbital semicircles in contact .... *antiquus*

3. Black oral melanin present 4

3a. Black oral melanin absent 5

4. Antehumeral mite fold lacking; tail bright lemon yellow (Fig. 31C; note: this feature may prove to be variable) .... *dickersonae*

4a. Antehumeral mite pocket present (Fig. 28); tail not bright lemon yellow .... *collaris* or *nebrius*

5. Posterior collar markings absent; anterior collar markings usually absent .... *insularis*

5a. Anterior and posterior collar markings present 6

6. White dorsal transverse bars present .... *vestigium*

6a. White dorsal transverse bars absent 7

7. Subadult females with orange tail; subadult and adult females with three melanic spots outlined in white along the lateral trunk surface .... *grismeri*

7a. Subadult females without orange tail; melanic spots outlined in white usually absent from lateral trunk surface .... *bicinctores*

Key to the Species of *Crotaphytus* (Juveniles)

1. Postfemoral mite pockets absent .... *reticulatus*

1a. Postfemoral mite pockets present (Fig. 29) 2

2. Antehumeral mite pocket absent .... *dickersonae*

2a. Antehumeral mite pocket present (Fig. 28) 3

3. Black oral melanin present .... *collaris* or *nebrius*

3a. Black oral melanin absent 4

4. A thin, pale tan dorsal caudal stripe is present and extends anteriorly onto the dorsal pelvic region ... *grismeri*

4a. A pale tan dorsal caudal stripe is lacking 5

5. Paired melanic keels on ventral surface of caudal extremity .. *vestigium* or *bicinctores* (variable in *bicinctores*)

5a. Paired melanic keels on ventral surface of caudal extremity lacking .... *insularis* or *bicinctores* (variable in *bicinctores*)

Key to the Species of *Gambelia* (Adults of Both Sexes)

1. Reddish male breeding coloration present; snout truncated; gular pattern in both sexes consists of grayish or black linearly arranged spots .... *silus*

1a. Male breeding coloration absent; snout elongate; gular pattern in both sexes consists of longitudinally oriented black streaks 2

2. Dorsal spotting extends onto the temporal region of the head and often to the terminus of the snout; dorsal base coloration off-white or pale tan (Fig. 30A) ..... *wislizenii*

2a. Dorsal spotting does not extend onto the dorsal surface of the head; dorsal base coloration dark brown or golden tan (Fig. 30B) .... *copei*

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Appendix 1

Specimens Examined

Museum acronyms follow Leviton et al. (1985) except for the following nonstandard abbreviations: BDH (collection of Bradford D. Hollingsworth), CES (Centro Ecologio de Sonora, Hermosillo, Mexico), EL (collection of Ernest Liner), JAM (collection of Jimmy A. McGuire), JMS (collection of Jay M. Savage), LLG (collection of L. Lee Grismer), MZFC (Museo de Zoología "Alfonso L. Herrera," Universidad Nacional Autónoma de México), REE (collection of Richard Etheridge), and UABC (Universidad Nacional Autónoma de Baja California, Ensenada, Mexico). The following abbreviations denote the form of preparation for each specimen: D (complete dry skeleton), S (skull only), P (preserved specimen), ARAB (alizarin red, alcian blue stained specimen), and H (hemipenis prepared by wax injection). Locality data are presented for all ingroup taxa examined but not for outgroup taxa.

Crotaphytidae

C. antiquus.—MEXICO: COAHUILA: CM 140199–140200; TNHC 53152–53154, 53157, 53160–53161 (P), 53155–53156, 53158–53159 (D), MZFC 6750–6756 (P)—Sierra de San Lorenzo, approximately 0.25 mi. W of the pueblo of Santa Eulalia.

Crotaphytus bicinctores.—UNITED STATES: ARIZONA: Coconino County: SDSNH 19479 (P)—Williams, 33053 (P)—5 mi. W Kane Ranch, 35812 (P)—Coconino, Lee's Ferry. Mojave County: USNM 115677 (D)–Rampart Cave. Maricopa County: REE 2921 (D)—6.3 mi. N Sentinel, 2922 (D)—2.3 mi. N Sentinel, 2923 (D), SDSNH 68624 (P)—7.0 mi. N Sentinel, 2924 (D)—3.2 mi. N Sentinel; SDSNH 68623 (P)—5.8 mi. N Sentinel, 68637–39 (P)—Extreme E slope Gila Bend Mtns. on W shore Gila River at jct. Old U.S. 80 and Gila River (W side Gillespie Bridge). Yuma County: LLG 1397–99 (P)—Trigo Mtns., 12 mi. W Palo Verde, REE 2931 (D)—Nr. Yuma Proving Grounds; SDSNH 16731 (P)—Castle Dome, 17602 (P)—Kofa Mtns., Wilbank Ranch, 22351 (P)—Sentinel, 26911 (P)—Plamosa Mtns., 33301 (P)—Dublin, 68625 (P)—Dome Valley Solid Waste Transfer Site, Co. 7th St., 1.0 mi. E Ave. 20E, NW of Wellton, 68626, SDSU 1723 (P)–S slope Laguna Mtns., 0.3 mi. NW Hwy 95 on rd. to N.R. Adair Park (and shooting range). CALIFORNIA: Imperial County: REE 2928–30 (D), SDSU 1721–22 (P)—S end Chocolate Mtns., jct. Ogilby Rd. and Hwy 86, REE 2925–27 (D)—jct. Palo Verde Mtns. and Hwy 78, 2933 (D)—Black Mtn., 2.8 mi. SSE Hwy 78 on Black Mountain Rd., 2934 (D), SDSNH 68627–28 (P, H), 68629–36 (P)—Chocolate Mtns., Black Mountain, Black Mountain Rd. Inyo County: AMNH 108970–71 (D)—9 mi. NE Big Pine, ca 6000'; SDSNH 15878–79 (P)—Death Valley, Furnace Creek, 15880–81 (P)—Death Valley, Stovepipe Wells, 15988 (P)—Argus Mtns., 3 mi. E Junction Ranch, 19475–77, 22218–19 (P)—Ballarat, 22220 (P)—Emigrant Pass, 34113 (P)—8 mi. SE Keeler, 34114 (P)—8 mi. W Panamint Spring, 34115 (P)—Wildrose Station, 34305 (P)—Independence, Mazurka Canyon, 38255–56 (P)—Panamint Mtns., Wildrose Station. Kern County: JMS 832 (S)—Twin Buttes nr. Mojave; REE 1570 (D)—2 mi. S Castle Butte. Riverside County: SDSNH 39751 (P)—3 mi. E Shaver's Summit, 39752 (P)—foot of Fanhill Canyon, 40139 (P)—4 mi. NE Whitewater. San Bernardino County: REE 2932 (D)—Ord Mtns; SDSNH 2459–61 (P)—Victorville, 4407 (P)—US Rt. 11 nr. California–Nevada line, 5874 (P)—Kramer Hills, 11087 (P)—N Fort Lytle Creek, 29091 (P)—Mountain Pass, 29229 (P)—7 mi. NE Cronise, 29664 (P)—Providence, Mtns., Cedar Canyon, 38703 (P)—20–50 mi. W Needles, 39874 (P)—Pipe Canyon. IDAHO: Owyhee County: SDSNH 1444–45 (P)—ID, Owyhee Co., Hot Springs S Bruneau. NEVADA: Clark County: JMS 203 (S)—Nr. Las Vegas. Lincoln County: USNM 18324 (D)—25 mi. E Panaca, nr. Utah line. Storey County: LLG 1400–01 (P)—Carson City. Washoe County: JMS 197 (S)—White Mt., Truckee Meadows, 198 (S)—E side Truckee Meadows. UTAH: Millard County: SDSNH 661–62 (P)—20 mi. NW Delta, 26704 (P)—10 mi. S Kanosh. Washington County: SDSNH 24982–83 (P)—Zion Nat. Park, 24984 (P)—St. George, 25506–07 (P)—7 mi. NW Santa Clara, 25508–09 (P)—Beaver Dam Mtns., 25644–46 (P)—Toquerville, 25647 (P)—Leeds, 25648–52 (P)—Rockville; UIMNH 27723 (S)—Springdale, 93994–95 (S)—Nr. St. George (nr. AZ border). No data: SDSNH 12244–45 (P).

C. collaris.—MEXICO: CHIHUAHUA: CM 59531 (P)—40 mi. E Julimes, 59532 (P)—18 mi. NE Aldama; KU 49628 (D)—Vado de Fusiles, 157873 (D), SDSNH 49753 (P)—22 km S Estacion Moctezuma, KU 157874 (D), SDSNH 49755 (P)—30.6 mi. S jct Mex. Hwys 45 and 49; REE 1213 (D)—20 mi. SW Chihuahua, 1214 (D)—6 mi. W Camargo; SDSNH 47932 (P)—Moctezuma, 47937–42 (P)—11–20 mi. N Chihuahua, 49754 (P)—11.6 mi. N jct. Mex. Hwys 45 and 49, 49756 (P)—12.7 mi. N jct. Mex. Hwys 45 and 49; UIMNH 48295 (S)—27.7 mi. S Ciudad Delicias. COAHUILA: CM 42936 (P)—8.6 mi. SW Cuatrocienegas de Carranza, N side San Marcos Mtn., 42938 (P)—4 mi. N Cuatrocienegas de Carranza, Rio Canon, 42939 (P)—5 mi. N Cuatrocienegas de Carranza, W slope Sierra del Muerto, 42940 (P)—5 mi. N Cuatrocienegas de Carranza, N end Rio Canon, 42941 (P)—E edge Cuatrocienegas Basin, along Hwy. 13.5 mi. E Cuatrocienegas de Carranza, 42942 (P)—Rancho San Fernando, 80 km SW Cuatrocienegas de Carranza; KU 147299 (D)—Motacorona; REE 2944 (D)—17.3 mi. E Viesca; SDSNH 49744 (P)—15.4 mi. S and 1.3 mi. W Sabinas, 49745 (P)—15.4 mi. S and 0.6 mi W Sabinas, 49746 (P)—0.9 mi. SE Motacorona, 49747 (P)—7.4 mi. N Ahuichila, 49748 (P)—5.8 mi. N Ahuichila, 49749 (P)—21.5 mi. SW Viesca, 49751 (P)—15.4 mi. S Sabinas, 6 mi. W, 49752 (P)—15.4 mi. S Sabinas, 3 mi. W, 56752 (P)—15.4 mi. S and 4.8 mi. W Sabinas; UIMNH 43224–25 (S)—15.6 mi. E Cuatro Cienagas; SDSU 2061 (P, H)—4.3 mi. N Bahia de Ahuichila, 2062 (P)—22.6 mi. S Viesca, 2063 (P)—4.8 mi. N Bahia de Ahuichila, 2064 (P)—1.3 mi. N Bahia de Ahuichila, 2065 (P)—15.1 mi. E Viesca. NUEVO LEON: CM 42943 (P)—2.7 mi. S Villa Garcia; SDSNH 56750 (P)—27.9 mi. N Mina. ZACATECAS: SDSNH 56751 (P)—1.1 mi. W Tecolotes. UNITED STATES: ARIZONA: Cochise County: AMNH 73518, 74752, 75657 (D)—Portal. Coconino County: AMNH 82297 (D)—11 mi. NNW Cedar Ridge; SDSNH 2087 (P)—16 mi. N Flagstaff, 9010, 29231 (P)—Canyon Diablo, 25503–05, 25639–40, 29131 (P)—Meteor Crater, 29645 (P)—Two Guns, 32529, 32658, 34466 (P), JMS 200 (S), UIMNH 34337 (S)—Wupatki Nat. Monument, JMS 202 (S)—The Citadel, Wupatki Nat. Monument; SDSNH 40958–59 (P)—1000 yds from Meteor Crater; UIMNH 27727 (D)—Wupatki Nat. Monument, nr. Citadel (4 mi. from Hwy 89). Gila County: SDSNH 27751 (P)—Sierra Ancha Mtns. Pima County: USNM 220214 (D)—Continental. Yavapai County: AMNH 84489, 85381, 85625 (D)—vicinity of Stanton. ARKANSAS: Brown County: SDSNH 40963–66 (P)—7 mi. N Harrison. County undetermined: USNM 220216 (D)—Red River. COLORADO: Delta County: CM 39257–39258 (P)—14 mi. NW Delta, Escalante Canyon. Fremont County: SDSNH 62106–13 (P)—Wet Mountain Project. Garfield County: JAM 315 (ARAB), REE 2871, 2874, 2879, (D) SDSU 1735, 2108 (P)—17.9 mi. N Hwy 70 via Hwy 139, REE 2878 (D)—18.5 mi. N jct. Hwys 139 and 70 via Hwy 139. Mesa County: CM 42932 (P)—Stovepipe Canyon, 2 mi. W, 17 mi. N Fruita, 42933 (P)—Colorado National Monument, mouth E Monument Canyon, 44747 (P)—Colorado National Monument. Montezuma County: CM 67094–67097 (P)—Bridge Canyon. San Miguel County: CM 42931 (P)—Disappointment Gap Spring (= Gypsum Gap). KANSAS: Cowley County: SDSNH 10982 (P)—7 mi. NE Winfield, 21859–63 (P)—2 mi. NE Winfield. Douglas County (?): REE 1797, 1823–24 (D)—nr. Lawrence. County undetermined: REE 1836, 1857 (D)—Kansas. NEW MEXICO: Colfax County: JMS 189 (S)—1.5 mi. N Chico post office, 7200′. Dona Ana County: REE 2945 (D)—Organ Mtns., 1.7 mi. S Hwy 82/70 on Baylor Canyon Dr., 2946–48 (D)—Organ Mtns., 5.1 mi. S Hwy 82/70 on Baylor Canyon Dr., 2949 (D)—Organ Mtns., 5.0 mi. S Hwy 82/70 on Baylor Canyon Dr.; SDSU 2059 (P)—Organ Mtns., 4.1 mi. S Hwy 82/70 on Baylor Canyon Dr. Eddy County: SDSU 2067 (P)—Carlsbad. Graham County: JMS 201 (S)—9.1 mi. ENE San Jose along new paved road to Clifton (1951). Hidalgo County: CM 75544–75551 (P)—ST 9, 3–5 mi. W Animas. Rio Arriba County: SDSNH 9007–08 (P)—Dixon, 57854 (P)—El Cobre Canyon. San Juan County: AMNH 108314 (D), SDSNH 20044 (P)—Chaco Canyon Nat. Monument. San Miguel County: JMS 190 (S)—10 mi. E Sanchez, 192 (S)—3.9 mi. NE Trementina. Torrance County: JMS 191 (S)—Manzano. OKLAHOMA: Cherokee County: SDSNH 52752–57 (P)—Tenkiller Ferry Reservoir. Jackson County: JAM 556 (P), REE 2951–52 (D)—Altus. TEXAS: Brewster County: SDSU 2058, 2066 (P)—2.3 mi. W Study Butte via Hwy 170. USNM 217271 (D)—specific locality unknown. Palo Pinto County: JMS 40, 195–96 (S)—Palo Pinto. Pecos County: JMS 194 (S)—Ft. Stockton. Presidio County: SDSU 2060 (P)—the River Road at the Teepees (W of Study butte). Reeves County (?): REE 2950 (D)—Pecos region. Shackelford County: Fort Griffin. Travis County: SDSU 2068–71 (P)—Milton Reimer's Fishing Ranch, 0.9 mi. from FM 3238 off Hwy 71. UTAH: Grand County: REE 2869, 2877 (D), SDSU 1734 (P, H)—33 mi. N jct Hwy 191 (NE Moab) via Hwy 128, REE 2870, 2875–76 (D), SDSU 2105–07 (P)—32.2 mi. N jct Hwy 191 (NE Moab) via Hwy 128; SDSU 2109 (P)—29 mi. NE Moab on Utah Hwy 128.

C. dickersonae.—MEXICO: SONORA: AMNH 78949 (P)—SE side Tiburon Island between Monument Pt. and red Bluff; BYU 2425, 39995 (P)—23 mi. N Kino Bay near coast, 2426, 2433, 3164, 3166–69, 3172 (P)—Punta Perla, NE end Tiburon Island; CAS 14008–12 (P)—Isla Tiburon, SE end, 53265 (P), JMS 208 (S)—Tiburon Island; REE 2774–77, 2787–88, 2904–05 (D), SDSU 1720, 2318 (P), 2319 (P, H)—1.2 mi. N Bahia Kino Nuevo via rd. to Punta Chueca, REE 2777–86 (D), SDSU 1718 (P)—Isla Tiburon, El Corralito, Appx. 3 km N of S end of island; SDSNH 47936 (P)—10 mi. N Bahia Kino; SDSU 1719 (P)—Isla Tiburon, Appx. 5 km N El Corralito (S end of island); UAZ 704–05, 30226 (P)—6.5 mi. by rd. NW Desemboque, 9625–26 (P)—Isla Tiburon, Ensenada Blanca, 16578 (P)—Bahia Kino, Mtn. NW Caverna Seri, 20144 (P)—Punta Cirio, 7.0 mi. by rd. S Puerto Libertad, 42569 (P)—Punta Cirio, Sierra Bacha, SE Libertad; USNM 238243–46 (P)—11.5 mi. N Punta Chueca, 238247–48 (P), 238249 (P, H)—4 mi. N Bahia Kino, 248142–43 (P)—Isla Tiburon, S end, 248174–80 (P)—3 mi. N Bahia Kino (Nuevo).

C. grismeri.—MEXICO: BAJA CALIFORNIA: Sierra de Los Cucapas: CES 067–624 (P), 067–627–29 (P), 067–25 (P, H); MZFC 6647–51 (D); UABC 115–19 (P)—Cañon David, appx. 2 km W Mex. Hwy 2 on the rd. to the Sulfur mine (turnoff at km 49 S Mexicali); USNM 37625 (P)—Volcano Lake.

C. insularis.—MEXICO: BAJA CALIFORNIA: CAS 14002 (P)—Isla Angel de La Guarda, SE end, 21948–49 (P)—Isla Angel de La Guarda, nr. small bay opposite Bay of Los Angeles (appx.

29°6′N, 113°12′W), 22712 (P)—Isla Angel de La Guarda: nr. small bay on SW shore, opp. Bay of Los Angeles (appx. 29°6′N, 113°12′W), 50873–79, 86754–55, 86783–84, 148650–52; REE 2793–97 (D), SDSU 1732 (P, H), 1733 (P)—Isla Angel de La Guarda, N end; SDSNH 19971, 19773–75, 50664, 53064 (P)—Isla Angel de La Guarda.

C. nebrius.—MEXICO: SONORA: AMNH 73715 (S)—Guaymas, 73758 (P)—16 mi. (via road) S of Nogales, 75682–83 (P)—Punta San Carlos, 7 mi. N Guaymas, 80852 (P)—2.3 mi. (road) NE Guaymas; BYU 40930–31 (P)—8 mi. N Guaymas; CAS 12774 (P)—31 mi. SW Moctezuma; KU 152639–42 (P)—139.4 km NW Caborca on Mex. Rt. 2, 176402 (P)—6.4 km S Guaymas; JMS 205 (S)—10 mi. S Hermosillo; LACM 8798 (P)—59.5 mi. E San Luis, 8799 (P)—84.1 mi. E San Luis; MVZ 10163–65 (P)—Sierra Alamo, 30 mi. W Caborca, 136687–88 (P)—1.9 rd. mi. N Bacadehuachi, 136689–90 (P)—ca 4.1 rd. mi. NW Nacori Chico; REE 370–71 (D)—nr. Pitiquito, 404–07 (D), 40 mi. W Sonoita, 2771–73 (D)—appx. 5 mi. N San Carlos Nuevo; SDSNH 49008 (P)—N bay at Guaymas; SDSU 2072 (P)—66.6 mi. W Sonoita, 2073 (P)—3.5 mi ENE Huasabas, 2074 (P)—5.2 mi. ENE Huasabas. UNITED STATES: ARIZONA: Maricopa County: SDSNH 68657–58 (P)—Buckeye Hills Recreation Area, above picnic area off Buckeye Hills Dr., 68659–61 (P)—Extreme W slope of Buckeye Hills on E side Gila River at jct. Old U.S. 80 and Gila River (E side Gillespie Bridge). Pima County: CAS 81420 (P)—20 mi. S Ajo, Alamo Canyon, Organ Pipe Nat. Monument; KU 121460 (P)—Gates Pass, Tucson Mtns. W Tucson; MVZ 76641 (P), UIMNH 5898 (S)—Ajo Mtns., Alamo Canyon, Organ Pipe Cactus Nat. Monument; REE 2937–38 (D)—SE edge Tucson Mtns., nr. end Sarasota Dr., 2939–41 (D)—Little Ajo Mtns., 2.9 mi. W Hwy 85 on entrance rd. to Ajo Air Force Station; SDSNH 68640–41 (P)—Ajo Mtns., ca 1.5 mi. S of Why, 68642–44 (P)—Quijotoa, 68645 (P), 68646 (P, H)—0.9 mi. S Why, 68647 (P)—4.1 mi. N Hwy 86 on rd. to Hickiwan, 68648–49 (P)—Silverbell Mtns., 20.4 mi. (by rd.) W Tucson Mtns. by way of Avra Valley Rd. Pinal County (?): KU 14860 (P)—20 mi. SW Phoenix. Yuma County: REE 2925 (D)—W face Gila Mtns., on Hwy 8, 4 mi. E Foothills Dr.; SDSNH 68650, 68652–54, SDSU 1724–25 (P)—W slope of Gila Mtns., ca 2 mi. N Hwy 8, SDSNH 68651 (P)—N slope Gila Mtns., 0.25 mi. S of RR tracks on S side Hwy 95 (at mile marker 39), 68655–56 (P)—Mohawk Mountains, N side Hwy 8.

C. reticulatus.—MEXICO: COAHUILA: SDSNH 56753 (P)—11.1 mi. S Villa Union. NUEVO LEON: EL 4138 (P)—5.9 mi. SSW 0.9–2.0 mi. NW Cerralvo along Rancho los Robles rd. to Picacho Mtns, 4816 (P)—6.2 mi. SW Cerralvo at Rancho Los Montemayores; JMS 211 (S)—between General Teran and El Carbendo; UIMNH 3983 (S), 3984 (P)—14 mi. E Cadereyta, Reynosa–Monterrey rd. TAMAULIPAS: 4130 (P)—Tamaulipas, 9.9 mi. SW Mier. UNITED STATES: TEXAS: County undetermined: KU 128993 (P)—7 mi. S Chacon Creek on Hwy 83 and 8 mi. NE on road to La Gloria Ranch. Dimmit County: KU 126948–52 (P)—26 mi. S Carrizo Springs on Hwy 186, San Pedro ranch. Maverick County: EL 3250.1–50.2 (P)—1 mi. E Eagle Pass on Manges Ranch; KU 481 (P)—Eagle Pass, 143567–69 (P)—1 mi. E Eagle Pass off U.S. Rt. 277, 147257 (P), 147266–76 (S), 147277–78, 157875–76 (D)—1 mi. E Eagle Pass, Manges Ranch; SDSNH 46884–86 (P)—2 mi. E Eagle Pass, 56754–55 (P)—1 mi. E Eagle Pass. McMullen County: CM 64677 (P)—4.1 mi. W jct. St. Hwy. 16 and FM 624 (ca 22 mi. SSW Tilden). Starr County: KU 9092 (P)—Arroyo El Tigre, ca Rio Grande City, 13202 (P)—Rio Grande City, 15388 (P)—23 mi. NW Rio Grande City; UIMNH 20336 (S)—Arroyo Los Alamos, 3 mi. SE Rio Grande City. Webb County: CM 52334–35 (P)—40 mi. WNW Laredo on FM 1472; EL 4748 (P)—21.8 mi. W Mirando City on Texas Rt. 359; KU 61447–49 (P)—40 mi. NW Laredo, 121487, 121489, 121491 (P)—5.2 mi. E jct. Hwys 44 and 83, 121488 (P)—10 mi. S Laredo, 126940–47, 126953–56, 126958 (P)—40 mi. WNW Laredo on FM 1472, Trevino Ranch, 128990 (P)—21 mi. NW I-35, ca Laredo on FM 1472, 128992 (P)—23 mi. NW I-35, ca Laredo on FM 1472, 7 mi. NE on El Chapote Rd.; REE 2906 (D)—37.0 mi. NNW Laredo on FM 1472, 2907 (D)—41.8 mi. NNW Laredo on FM 1472, 2908 (D)—25.3 mi. NNW Laredo on FM 1472, 2909 (D)—34.4 mi. NNW Laredo on FM 1472, 2910 (D)—36.0 mi. NNW Laredo on FM 1472, 2911 (D)—19.6 mi. NNW Laredo on FM 1472, 2912 (D)—35.7 mi. NNW Laredo on FM 1472, 2913 (D)—22.6 mi. NNW Laredo on FM 1472; SDSNH 41333 (P)—about 10 mi. S Laredo. Zapata County: KU 13203 (P)—San Ignacio.

C. vestigium.—MEXICO: BAJA CALIFORNIA: CAS 14000–01 (P)—Vicinity Bahia de Los Angeles, 154267 (P)—7 km W (by rd.) of Bahia de Los Angeles; JMS 207 (S)—El Marmol, 210 (S), SDSNH 43226 (P)—Sierra de Juarez, Cantillas Canyon; REE 2806 (D)—1.5 mi. N Bahia de San Luis Gonzaga, 2807–08 (D)—Sierra Las Pintas, 2810 (D)—10 km W Bahia de Los Angeles, 2814 (D)—1 km W Bahia de Los Angeles, 2815 (D)—1.5 km S of hwy to Bahia de Los Angeles at km marker 56, 2822 (D)—46 km W int. Mex. Hwys 3 and 5 on Hwy 3, 2823 (D)—Sierra San Felipe, Campo La Roca, 18.5 mi. S San Felipe, 2824 (D)—20 mi. NW San Felipe, int. powerlines and Sierra San Felipe, 2936 (D)—28.5 mi. N Bahia de Los Angeles; SDSNH 17052 (P)—S base of Sierra de Juarez, 17667 (P)—San Borja, 24391–92 (P)—San Jose, 26754 (P)—E side Sierra San Pedro Martir, Cañon del Cardones, 37815 (P)—1 mi. NW San Felipe, 41612 (P)—appx. 2.5 mi. W Bahia de Los Angeles, 45978 (P)—SE Mesa de San Carlos, 52950–51 (P)—Bahia de Los Angeles, 1.8 mi. S of V.S.E. Field Station; SDSU 1726–27 (P)—5 km E El Parador on rd. to Bahia de Los Angeles, 1728 (P)—W base Sierra La Asamblea, appx. 20 mi. N El Parador. BAJA CALIFORNIA SUR: CAS 18822 (P)—BCS, 9 mi. W San Ignacio, 146684 (P)—Santa Agueda, 147683 (P)—29.1 mi. S (by rd.) Mulege on Mex. Hwy 1, 154268–70, 154272 (P), 154271 (P, H)—Santa Agueda; REE 2809 (D)—9.7 mi E San Isidro, 2811 (D)—16 km S Mulege, 2812 (D)—2 km E San Jose de Magdelena, 2813 (D)—1 km E San Jose de Magdelena, 2816–17 (D)—km marker 76 N Loreto, 2818 (D)—Km 28 E Mex. Hwy 1 on rd to San Francisco de La Sierra, 2819 (D)—7.6 mi. E San Isidro, 2820 (D)—5.4 mi. E San Isidro, 2821 (D)—3.0 mi. E San Isidro, 2825 (D)—17.2 mi. S by rd. of San Jose de Comondu, 2826 (D)—13.2 mi. S by rd. of San Jose de Comondu; SDSU 1729 (P)—10.6 mi. S San Jose de Comondu, 1730 (P)—Rd. to San Francisco de La Sierra. UNITED STATES: CALIFORNIA: Imperial County: JAM 41 (ARAB)—Inkopah Trail, 2 mi. E Jacumba; REE 2935 (D)—Mountain Springs, N side westbound Hwy 8. Riverside County: BYU 2422, 2430, 2432, 2435, 2438 (P)—Chino Canyon, W Palm Springs. San Diego County: CAS 7930 (P)—Palm Canyon, 62794–95 (P)—San Felipe Creek, 62875 (P)—Mason Valley; JAM 617–18 (P)—Vallecitos Co. Park, McCain Pit; JMS 199 (S)—Sentenac Canyon, 204 (S)—3.5 mi. E Jacumba, 209 (S)—Borrego Mtn. No data: SDSNH 19788–92 (P).

Gambelia copei.—MEXICO: BAJA CALIFORNIA: MVZ 31794–95 (P)—3 mi. W Canyon de Llanos, ca 10 mi SW Alaska (= Rumarosa), 31839 (P)—6 mi. W Alaska (= Rumarosa), 140759 (P)—Sierra San Pedro Martir, 2 mi. SW Paseo de San Matias;

REE 2800 (D)—1.0 km N San Borja; SDSNH 4071 (P)—San Jose, San Telmo River, 4143 (P)—3 mi. E. San Telmo, 5078–80, 26752–53 (P)—San Jose, 5264, 15969 (P)—Isla de Cedros, S. end, 7249, 17411, 24340–42 (P)—Isla de Cedros, 18118 (P)—Bahia de San Francisquito, 18945–46 (P)—Valle de Trinidad, 19787 (P)—40 mi. W Bahia de Los Angeles, 27693–94 (P)—Isla de Cedros, canyon N middle canyon, 27965 (P)—Isla de Cedros, Middle Canyon, 41613 (P)—Mouth of Arroyo de Rosario, 42622 (P)—2 mi. N. San Simon, 43007 (P)—8 mi, E. El Rosario, 45916 (P)—NE Mesa de San Carlos. BAJA CALIFORNIA SUR: CAS 56105 (P)—Isla Santa Margarita, 147738–39 (P)—1.3 mi. NE Punta Abreojos, 147750 (P)—SE Sierra Santa Clara; REE 2798 (D)—km 24.5 on rd. to Punta Abreojos, 2799 (D)—Sierra Santa Clara, 2801 (D)—jct. rds. to Puerto Nuevo and Bahia Tortuga, 2802 (D)—km 57 W of Mex. Hwy 1 on rd. to Punta Abreojos, 2803 (D)—Sierra Santa Clara, Rancho Santa Clara, 2804 (D)—Sierra Santa Clara, 1.0 mi. S Rancho San Ramon, 2805 (D)—km 30.25 on rd. to Punta Abreojos; SDSNH 17470 (P)—El Arco, Miraflores Rancho. UNITED STATES: CALIFORNIA: San Diego County: CAS 40302, 57865 (P)—Campo, 62964 (P)—Potrero Grade; SDSNH 55251 (P)—1.5 mi. NE Cameron Corners.

G. coronat†.—UNITED STATES: CALIFORNIA: San Diego County: LACM 7058/42880 (S)—Anza Borrego Desert State Park.

G. silus.—CALIFORNIA: Fresno County: CAS 22713 (D), 22714 (D, H)—in dry Panoche Creek bed, mouth of canyon on W side San Joaquin Valley (about 120°39′W, 36°38′N), 20 mi. by rd. WSW Mendota, 23250 (H)—nr. foothills, 3 mi. SE mouth of Panoche Canyon and 16.5 mi. SW Mendota, next to pole line rd., "Staggeredrock trap station," 141318–19 (D)—20.2 mi. S jct. Cal Hwys 33 and 180, and 1.7 mi. W on dirt rd. (nr. three Rocks); KU 121493 (P), 121751 (S)—Bundgard Ranch, 10 mi. ESE Mendota, 121500 (P)—8 mi. ESE Mendota ca Double C Ranch, 121504 (P), 121752–53 (S)—9 mi. ESE Mendota at Double C Ranch, 121507 (P)—121520, 121526–27 (P)—2 mi. SW jct. Interstate 5 and Shields Ave. on Panoche Plain, 121524 (P), 121510 (S)—Mouth of Little Panoche Creek on Levy-Zentner Ranch, 121754 (S)—2 mi. S jct. Shields Ave. and Little Panoche Rd., 121755–56 (S)—2 mi. SSE jct. Shields Ave. and Little Panoche Rd., 121758–60, 121762 (S)—1 mi. NW Three Rocks, 15 mi. S Mendota, 121764 (S)—Levy-Zentner Ranch, 1 mi. E mouth Little Panoche Creek, 121765 (S)—3 mi. N Mercey Hot Springs along Little Panoche Creek, 121766 (S)—2 mi. S jct. Interstate 5 and Shields Ave, 121767–68 (S)—Levy-Zentner Ranch, Little Panoche Wash. Fresno County (?), 2 mi. S turnoff to Little Panoche Ranch on Little Panoche Rd., 121511 (P), 121757 (S)—Little Panoche Ranch turnoff on Little Panoche Rd. Kern County: KU 121769–75 (S)—Blackwell's Corner, 30 mi. W Wasco, jct Hwys 33 and 46; SDSNH 16055–59 (P)—3 mi. N McKittrick, 42434–35 (P)—W end Greenhorn Mtns, 46339 (P)—Bakersfield. Kings County: JMS 206 (S)—2 mi. S Kettleman City; SDSNH 31697 (P)—Wheeler Ridge Post Office. Madera County: KU 121605, 121610, 121615–16 (P)—8 mi. E Firebaugh, 121623 (P)—4 mi. E Firebaugh on Rd. 9, 121748, 121750 (S)—8 mi. E Firebaugh off Ave. 7 1/2, 121749 (S)—12 mi. E Firebaugh; SDSNH 46888–89, 49758–59 (P)—5.9 mi. E Firebaugh. Merced County: KU 121631–34, 121636–38 (P)—4.5 mi. NW jct. Hwy. 152 and Hwy. 59, Red Top, 121644–46, 121648 (P)—10 mi. SW Los Banos on Arburua Rd., 121647 (P)—9 mi. SW Los Banos on Arburua Rd., 121649 (P)—W jct. Arburua and Langdon Rds., 121650–51 (P)—8.7 mi. S Los Banos off Mercy Springs Rd., 121652 (P)—10 mi. SW Los Banos, W jct. Arburua and Langdon Rds. San Benito County: CAS 22724–25 (D)—in and about the dry wash, SE end Panoche Valley; KU 121537 (P)—2 mi. N jct. Little and Big Panoche Rds. San Luis Obispo County: CAS 23195 (H)—Carrizo Plain, dry creek at N end of false valley between Panorama Hills and the Temblor Mtns., 13 mi. at 235 degrees from Simmler; KU 121657 (P)—0.3 mi. W and 0.2 mi. S jct. CA Rts. 33 and 166, 121658 (P)—1.7 mi. E jct. CA Rts. 33 and 166, 121659 (P)—Cuyama Valley at jct. CA Rts. 33 and 166, 121662 (P)—7.8 mi. N jct. Soda Lake Rd. and CA Rt. 33, 121664 (P)—7.5 mi. N jct. Soda Lake Rd. and CA Rt. 33, 121671 (P)—7 mi. W Maricopa.

G. wislizenii.—MEXICO: BAJA CALIFORNIA: BYU 23336 (P)—5 mi. N. San Felipe, 34513 (P)—3 mi. S. San Felipe (by rd. to Puertocitos), 34514 (P)—2.9 mi. S. San Felipe (by rd. to Airport), 34515 (P)—4 mi. W. San Felipe (at trash dump); CAS 90256 (P)—San Felipe-Ensenada Rd. (Mex. Hwy. 3), 6.8 mi. W. of San Felipe-Mexicali Hwy (Mex. Hwy 5), 119100 (P)—Mouth of Guadalupe Canyon; LACM 94813 (P)—Arroyo Matomi, 132230 (P)—N. end Laguna Salada, 132231 (P)—3 mi. N. Pozo Penara, Laguna Salada; MVZ 9589 (P)—E. base San Pedro Martir Mountains, El Cajon Canyon, 50017 (P)—Punta San Felipe, 182117 (P)—5.8 mi. N. San Felipe (via Mex. Hwy. 5). CHIHUAHUA: UIMNH 6672–73 (S)—28.7 mi. S Samalayuca, 40408 (S)—sand dunes 35 mi. S Juarez, 43373–75 (S)—6.8 mi. S Samalayuca, 43383 (S)—0.3 mi. E Carillo. COAHUILA: EL 3129 (P)—5.2 mi. S. Cuatrocienegas de Carranza along Rio Mesquites; UIMNH 43378 (S)—7 mi. E Matamoros. DURANGO: UIMNH 43379 (S)—13.5 mi. S Tlahualilo. SONORA: CAS 15347 (P)—1.5 mi. W Altar, 15356 (P)—4.7 mi. SSE La Playa, 17049–50 (P)—Isla Tiburon, SE end of island, 104451 (P)—Isla Tiburon, SW end; REE 2789–91 (D)—Isla Tiburon, appx. 2 mi. N El Corralito (S end of island); SDSNH 38251 (P)—3 mi. NE Punta Peñasco, 38252 (P)—16 mi. NE El Papalote, 38253 (P)—18.5 mi. NE El Papalote, 38254 (P)—12 mi. NE Punta Peñasco, 38605 (P)—El Papalote, 38606 (P)—1 mi. NE El Papalote, 38888 (P)—12 mi. NE Punta Peñasco, 40601 (P)—24 mi. N Punta Peñasco, 49009 (P)—36 mi. E. San Luis. UNITED STATES: ARIZONA: Coconino County: SDSNH 6030–32 (P)—Grand Falls of Little Colorado River, 32560 (P)—Nr. Jacob Lake, 35813–14 (P)—3 mi. SW Navajo Bridge. Maricopa County: JMS 187 (S)—Wickenburg. Yuma County: REE 810 (D)—Yuma County. Undetermined: USNM 220224 (D)—Arizona. CALIFORNIA: Imperial County: REE 1029, 1172 (D)—Glamis, 2915 (D)—Salton City; SDSNH 1879 (P)—5 mi. E. Holtville, 7143 (P)—4 mi. N. Kane Spring, 7847 (P)—Kane Spring, 10937 (P)—Mountain Spring, 11346 (P)—Coyote Wells, 13352 (P)—4 mi. N. Bard, 13911, 20967 (P)—Gray's Well, 18596 (P)—6 mi. N. Truckhaven, 28762 (P)—Niland, 36541 (P)—Ocotillo, 39735 (P)—5 mi. E San Diego-Imperial Co. line, 49002 (P)—17.5 mi. W. Calexico, 49003 (P)—3 mi. E. Coyote Wells. Kern County: USNM 18298 (D)—Kernville. San Bernardino County: CAS 190054 (H)—Kelbaker Rd., 2.6 mi. SE Baker; JMS 41 (S)—29 Palms; REE 1571 (D)—17 mi. ESE Lucerne Valley, 2916–17 (D), SDSNH 68662, 68664 (P)—Hinkley, Hinkley Rd, REE 2918–20 (D), SDSNH 68663, SDSU 2282 (P)—Johnson Valley, Camp Rock Rd; SDSNH 23636 (P)—Stoddard Well. San Diego County: JMS 21, 186 (S)—Clark Dry Lake, 184 (S)—Borrego Valley, 185–1,2 (S)—Split Mountain, 188 (S)—14 mi. E Benson's Dry Lake. County undetermined: REE 496, 550 (D) California. IDAHO: Ada County: SDSNH 1450–51 (P)—Ada Co., foothills N. of Boise. Elmore County: SDSNH 1452 (P)—S. of Cleft. NEVADA: Nye County: UIMNH 93992–93 (S)—15 mi. N Mercury. Storey County: REE 2914 (D)—Carson City. Washoe County: UIMNH 3166 (S)—20 mi.

N Reno, 3167–68 (S)—5 mi. S Sutcliffe, Pyramid Lake, USNM 220226 (D)—Sutcliffe, Pyramid Lake. County undetermined: Nevada. camp 12. NEW MEXICO: Luna County: EL 5176 (P)—4.2 mi. S., 0.6 mi. E. Deming on Rock Hound State Park road. UTAH: Javier County: JMS 183 (S)—2 mi. W Monroe. San Juan County: CAS 141349 (H)—10.8 rd. mi. N Montezuma Creek. No locality: JMS 700 (D).

Chamaeleonidae

Brookesia kersteni: REE 532 (D). *B. stumpffi:* REE 1911 (D). *Hydrosaurus amboiensis:* REE 2068 (D), 2080 (D); SDSNH 47009 (D). *H. pustulatus:* CAS 11000–01 (P), 28171 (P), 62377 (P), 85642 (P). *Leiolepis belliana:* REE 1680 (D), 1906 (D), 1908 (D), 1993 (D), 2505 (D); SDSU 2587–90 (P). *Physignathus cocincinus:* SDSNH 67845 (D), 68062 (D). *P. lesueurii:* KU 69303 (S, P), 69304 (P); REE 1364 (D), 1722 (D), 1849 (D). *Uromastyx acanthinurus:* CAS 135162 (P), 135166–67 (P); KU 94507 (S, P); REE 318 (D), 450 (D); SDSNH 62665 (D). *U. aegyptius:* SDSU 2584 (P). *U. asmussi:* CAS 154357 (P). *U. benti:* SDSNH 68121 (D). *U. geyrii:* CAS 135006–16 (P). *U. hardwickii:* REE 1339 (D), 1840 (D); SDSU 2573–78 (P). *U. loricatus:* CAS 86379 (P), 86463 (P), 120480 (P). *U. macfadyeni:* SDSU 2580 (P). *U. microlepis* (synonymized with *U. aegyptius* by Moody, 1987): CAS 97834–35 (P); SDSNH 55288 (D); SDSU 2585–86 (P). *U. ocellatus:* SDSU 2582–83 (P). *U. philbyi:* CAS 139537 (P), 141997–98 (P); SDSU 2579 (P). *U. thomasi:* CAS 190887 (P); SDSU 2581 (P).

Corytophanidae

Basiliscus basiliscus: KU 84956 (D), 93452–54 (D); REE 2015 (D). *B. plumifrons:* KU 25660 (P), 91784 (P), 96637 (P), 180368 (P); REE 427 (D), 2014 (D); SDSNH 57098 (D), 57100 (D); SDSU 2093 (P). *B. vittatus:* REE 49 (D), 555 (D), 637 (D), 1601 (D), 1729 (D), 1757 (D), 1759 (D); SDSU 2095–96 (P). *Corytophanes cristatus:* KU 59602 (P); SDSNH 62345 (D), 67849–50 (D); SDSU 2098–2100 (P). *C. hernandezi:* KU 24068 (P), 24070–71 (P), 24073 (P); REE 1176 (D), 1800 (D); SDSNH 68090 (D). *C. percarinatus:* KU 93456 (S), 184183–84 (P), 187149–50 (P), 190773 (D). *Laemanctus longipes:* KU 27529 (P), 59608 (P), 187739 (P); SDSNH 64542 (D), 67835 (D), 68086 (D). *L. serratus:* KU 70226 (P), 70267 (P), 74910 (D), 75532 (P); REE 619 (D); SDSU 2095 (P).

Hoplocercidae

Enyalioides laticeps: KU 125967 (D), 147929–34 (P), 147937 (P), 147939–42 (P), 152497–98 (P); REE 76 (D); SDSU 2116–17. *E. oshaughnessyi:* KU 122116 (P), 147183 (P); REE 1957 (D). *E. praestabilis:* KU 122117 (P), 140394 (P), 147184 (P), 169854 (P).

Iguanidae

Brachylophus fasciatus: REE 1019 (D), 1866 (D), 1888 (D); SDSNH 55601 (D), 55603 (D); SDSU 2591–93 (P). *Dipsosaurus dorsalis:* JAM 287 (D), 345–51 (D); SDSU 2594–600 (P).

Opluridae

Chalaradon madagascariensis: KU 187757 (P), 187762–63 (P), 187765 (P), 187756 (S); REE 455 (D), 457 (D), 547 (D); SDSU 2123–29. *Oplurus cuvieri:* JAM 281 (D); KU 187666–68 (P); REE 558 (D), 620 (D), 1835 (D). *O. cyclurus:* CAS 86739 (P). *O. fierinensis:* KU 187769 (P), 187770 (S,P), 187771–72 (P). *O. quadrimaculatus:* REE 658 (D); SDSU 2120–22 (P). *O. saxicola:* CAS 13958 (P), 14439 (P), 86724 (P); SDSU 2119 (P).

Phrynosomatidae

Callisaurus draconoides: JAM 88 (D), 184 (D), 202 (D), 361 (D). *Petrosaurus mearnsi:* JAM 285 (D), 288–90 (D), 295 (D); REE 351 (D), 557 (D); SDSU 2253 (P). *P. repens:* SDSNH 17484 (P), 45985 (P). *P. thalassinus:* REE 575 (D), 765 (D); SDSNH 17484 (P), 32922 (P), 44516 (P), 45985 (P). *Phrynosoma asio:* REE 1489 (D), 1580 (D), 1676 (D); SDSU 2308–09 (P). *P. coronatum:* REE 310 (D), 390 (D), 527 (D), 609 (D), 1438–39 (D), 1786 (D), 1999 (D); SDSNH 16042–43 (P); SDSU 2305–07 (P). *P. ditmarsi:* SDSU 2278 (P). *P. douglassi:* REE 1109–11 (D), 1118 (D), 1372 (D); SDSU 2283–84 (P). *P. orbiculare:* REE 1104 (D), 1181 (D), 1725 (D), 1920 (D), 1931 (D). *Uma exsul:* REE 2880–81 (D); SDSU 2274–77 (P). *U. inornata:* KU 90961 (D), 95849 (D); REE 263–64 (D), 602 (D),1538 (D); SDSNH 2754 (P), 48486 (D). *U. notata:* JAM 172 (D), 235–37 (D), 239–41 (D); SDSU 2558–63 (P). *U. scoparia:* BDH 117 (D); CAS 42135 (S); REE 509 (D), 551 (D), 2867 (D); SDSNH 7556 (P), 7658 (P), 38419 (P). *Urosaurus auriculatus:* SDSNH 34853 (P), 34859 (P), 34861 (D), 34866 (P). *U. bicarinatus:* SDSNH 7371 (P), 10154 (P), 28513 (P). *U. clarionensis:* SDSNH 22514 (P), 22529 (P), 28507 (P). *Uta nolascensis:* CAS 14244 (P), 14247–48 (P). *U. palmeri:* SDSNH 46492–94 (P), 46496 (P). *U. squamata:* CAS 52343 (P), 52351 (P), 52359 (P). *U. stansburiana:* JAM 265 (D), 284 (D), 301 (D), 366 (D); REE 274–75 (D), 1877–78 (D); SDSNH 3374 (P), 60800–110 (P), 60800–187 (P), 60800–418 (P); SDSU 2525–30 (P).

Polychrotidae

Anisolepis grilli: REE 1952 (D); SDSU 2130–31 (P). *Chamaeleolis chamaeleonides:* CAS 14610 (P); KU 245644 (P). *C. porcus:* KU 245645. *Enyalius bibronii:* MCZ 163783 (P). *E. bilineatus:* MCZ 5567, 84034, 144556, 163776, 163777 (P); REE 1678 (D), 1958 (D). *E. boulengeri:* MCZ 163780 (P), 163781 (D). *E. brasiliensis:* MCZ 3317, 3322, 4251, 163778–79 (P); REE 1960 (D). *E. catenatus:* CAS 16101 (P); MCZ 163782 (P); REE 1961 (D). *E. iheringii:* MCZ 6315, 163786–87 (P); REE 1959 (D); SDSU 2222–23 (P). *E. perditus:* MCZ 163788 (D), 163789 (P). *E. pictus:* MCZ 82873 (P), 163784 (D), 163785 (P); SDSU 2221 (P). *Phenacosaurus heterodermis:* SDSU 2224–25 (P). *P. richteri:* SDSU 2226–27, 2240 (P). *Polychrus acutirostris:* KU 73436–38 (P); MZUSP 568 (D), 4412 (D), 4448 (D), 4543 (D); SDSU 2236–37 (P). *P. femoralis:* KU 142682 (P), 218381 (P). *P. guttarosus:* KU 25170 (P), 76074 (P), 113495 (P); SDSU 2235 (P). *P. liogaster:* KU 133872–73 (P). *P. marmoratus:* JMS 116–117; REE 346 (D), 2283 (D), 2496 (D), 2498 (D), 2863 (S); SDSU 2231–34 (P). *Pristidactylus casuhatiensis:* MCZ 162924 (D). *P. torquatus:* CAS 85234 (D); MCZ 33586 (D); REE 2766–68 (D); SDSU 2249–51 (P). *Urostrophus vautieri:* CAS 13883 (P); REE 2507 (D); SDSU 2522 (P).

Tropiduridae

Ctenoblepharys adspersus: LACM 49147 (D); MVZ 85415–16 (P); REE 2513 (D). *Leiocephalus carinatus:* REE 1469 (S), 1805–06 (D), 1816 (D); SDSNH 67957–58 (P); SDSU 1996–97 (P). *L. greenwayi:* REE 1814 (D). *L. inaguae:* KU 242855 (P), 242859 (P), 242865 (P), 242868 (P). *L. macropus:* REE 1819 (S); SDSNH 65959–60 (P), 65989 (D), 66002 (P), 66004–05 (D), 66012 (P). *L. melanochlorus:* KU 243460 (P), 243463 (P), 243470 (P), 243474 (P); REE 1802 (D). *L. pratensis:* KU 244861–62 (P), 244864 (P), 246145 (P). *L. psammodromus:* KU 244836 (P), 244838–39 (P), 244843 (P); REE 1813 (D). *L. schreibersi:* KU 245006–08 (P); REE 1808 (D); SDSNH 64665 (D), 64668–69 (D), 64672 (P), 64675 (P), 66967 (P), 66970 (P); SDSU 1998 (P). *Microlophus duncanensis:* CAS 12202 (D). *M. grayi:* CAS 11620 (D). *M. stolzmanni:* KU 134701 (P), 134712 (P), 134743–44 (P). *M. theresioides:* KU 162010–11 (P), 162015–16 (P). *M. tigris:* KU 163750–52 (P), 163757 (P). *Phymaturus palluma:* REE 2306 (D), 2309 (D), 2311 (D), 2313 (D), 2326 (D); SDSU 1946–51 (P). *P. patagonicus patagonicus:* REE 2471-72 (D); SDSU 1980 (P). *P. p. payuniae:* REE 2331-33 (D), 2336 (D), 2339 (D), 2360 (D); SDSU 1981–84 (P). *P. p. somuncurensis:* REE 2433–36 (D), 2439 (D); SDSU 1780–84 (P). *P. p. zapalensis:* REE 2451-53 (D); SDSU 1986–90 (P). *P. punae:* REE 2356–7 (D), 2383–85 (D); 1978–79 (P). *P.* sp.: SDSU 1991–95 (P). *Plesiomicrolophus koepckeorum:* KU 163604 (P), 163606–07 (P), 212665 (P). *Stenocercus guentheri:* SDSNH 49472 (P). *Uranoscodon superciliosus:* KU 128214 (P), 128215 (D), 128216 (P), 128218 (P), 130218 (P), 135269 (D); REE 2589 (D); SDSNH 65497 (D); SDSU 2110 (P).

APPENDIX 2

Data Matrix

The symbols a–y represent frequency ranges within which the derived character state was observed in any particular terminal taxon (see Table 1). "?" = missing or unknown.

		1	11111	11112	22222	22223	33333	33334	44444
	12345	67890	12345	67890	12345	67890	12345	67890	12345
Ancestor	aaaa?	aa??a	aa?aa	a??a?	?a??a	aa0aa	?aa??	a?aaa	aaaaa
G. copei	yyayy	yyaay	ypayy	ayaaa	yaayy	ya0yy	Cwaaa	yaaah	ydyyy
G. corona†	a?a?y	?aaa?	?y???	a?aaa	?y??y	ya0?y	Dya??	?a???	?????
G. silus	fyaya	ydaac	ayaym	axaay	ya?w?	ya0yy	Anaaa	yauaa	ukyyy
G. wislizenii	yyayy	ycaax	yyayy	awaaa	yaayy	ya0yy	Bvaaa	qaaae	xfyyc
C. bicinctores	babya	yayyy	aayya	aaayy	ay?aa	by1ya	Lkyyy	ayayy	byyde
C. antiquus	agmya	yayys	aayya	aaayy	ayyaa	ay1ya	Fsysy	gyaay	ayyym
C. collaris	abaya	yayyy	aayya	avayy	axyba	cy1ya	Gkyyy	ayaay	asyaa
C. dickersonae	aayya	yayyy	aayya	aayyy	ayyaa	dy1ya	Isyyy	ayayy	ayyai
C. grismeri	faaya	yayyy	aayya	akayy	ay?aa	ay1ya	Jkyyy	ayayy	auyfp
C. insularis	yaaya	yayyy	aayya	yaayy	ayyaa	yy1ya	Kayyy	ayayy	ayyfa
C. nebrius	aaaya	yayyy	aayya	aaayy	ayyda	by1ya	Hsyyy	ayaay	axyaa
C. reticulatus	aaaya	yayyy	aayya	aeayy	ayyca	cy2ya	Eqyyy	ayaay	awqay
C. vestigium	baaya	yayyy	aayya	jaayy	ayyba	gy1ya	Mkyyy	ayayy	axydc

APPENDIX 2—*Extended*

44445 67890	55555 12345	55556 67890	66666 12345	66667 67890	77777 12345	77778 67890	8888 1234	8 5	88889 67890	99999 12345	999 678
yaaaa	aaaa?	?aa?a	aaaaa	aa??a	aa???	aa?a?	??a0	?	?aa??	?????	???
aaaay	ayyay	aayay	ayaaa	aa0aa	ya???	aa?a?	?ya0	(04)	a?a??	?????	???
?????	?????	?????	?????	?????	?????	?????	????	?	?????	?????	???
yaaaa	ayaay	aayaa	ayaya	aa0aa	ya???	aa?a?	?ya0	0	aaa??	?????	???
yaaaa	ayyay	aayay	ayaaa	aa0aa	ya???	aa?a?	?ya0	0	ayall	11111	111
ayayy	vaaya	yyyya	yaaay	yy2yL	ayay2	ayyay	aas0	4	yay44	44444	444
ayayy	yaaya	yyyya	??aya	yylyy	yyay(012)	yyayy	aaa0	4	ya???	?????	???
gtayy	eaaya	yyyya	yaaaa	ya2yh	yyaa(01)	thaaa	aac(03)	(345)	yay66	66666	666
ayyyy	yaaya	yyyya	yayay	ya2yy	yyayl	ayyay	aaa3	3	yay22	22222	222
ayayy	yaaya	yyyya	yaaay	ya2yy	ayay2	ayyay	aaa0	4	yay??	?????	???
apayy	yaaya	yyyya	yaaay	ya4ya	ayyy3	ayyay	aapl	4	yay??	?????	???
awayy	yaaya	yyyya	yaaaa	ya2yy	yyay0	gyaaa	xas2	2	yay55	55555	555
avayy	aaaya	yyaya	yaaaa	yalaa	yyyy(01)	ta?yy	aaa0	1	aay77	77777	777
ayayy	yaaya	yyyya	yaaay	ya3yy	ayyy3	ayyay	aau(12)	4	yay33	33333	333

APPENDIX 3

Outgroup Data Matrix

Species that exhibited more than one character state were assigned state V (variable) in this data matrix. "?" = missing or unknown.

		1	11111	11112	22222	22223	33333	33334
	12345	67890	12345	67890	12345	67890	12345	67890
Brookesia stumpffi	0?10?	000??	?0100	0110?	01??1	00000	?0???	????1
Chamaeleo kersteni	0?00?	001??	?0000	0110?	0???1	00000	?0???	????1
Hydrosaurus amboiensis	0000?	10110	00000	0010?	?01?0	00200	?0?01	??001
H. pustulatus	?????	?????	?????	?????	?????	?????	?????	????1
Leiolepis belliana	0000?	00110	00011	0110?	011?0	10000	?0?00	V?001
Physignathus cocincinus	0000?	10110	?0000	0110?	001?0	00000	?0???	??001
P. lesueurii	0000?	10110	00010	0111?	001?0	00000	?0?01	0?001
Uromastyx acanthinurus	0000?	V00V0	00000	0111?	101?1	01000	?0???	??00V
U. aegyptius	?????	?????	?????	?????	?????	?????	?????	?????
U. asmussi	?????	?????	?????	?????	?????	?????	?????	????1
U. benti	0000?	00010	00000	0?11?	1?1?1	00000	?0???	??001
U. geyrii	?????	?????	?????	?????	?????	?????	?????	????1
U. hardwickii	0?00?	?0000	00000	011??	001?1	00000	?0?0?	??001
U. loricatus	?????	?????	?????	?????	?????	?????	?????	????1
U. mafadyeni	?????	?????	?????	?????	?????	?????	?????	????1
U. microlepis	0000?	00010	00000	0111?	101?1	01000	?0???	??001
U. ocellatus	?????	?????	?????	?????	?????	?????	?????	????1
U. philbyi	?????	?????	?????	?????	?????	?????	?????	????1
U. thomasi	?????	?????	?????	?????	?????	?????	?????	????1
Chamaeleonidae	0000?	00110	00000	0110?	001??	00000	?0?0?	0?001
Basiliscus basiliscus	0000?	10110	00000	0000?	10100	00000	?001?	1?100
B. plumifrons	0000?	10110	00000	0010?	10100	00000	?001?	1?100
B. vittatus	0000?	101?0	00000	0010?	101?0	00000	?001?	1?100
Corytophanes cristatus	0000?	101V0	?0000	0010?	?0100	00000	?0V1?	1?101
C. hernandezi	0V00?	10110	?0V00	0V10?	000?0	00000	?00??	1?101
C. percarinatus	0000?	10110	?0V00	0110?	0?100	00000	?01??	??101
Laemanctus longipes	0000?	101V0	00000	0010?	V0V00	00000	?001?	1?101
L. serratus	0000?	10110	00000	0100?	00100	00000	?0V1?	??101
Corytophanidae	0000?	101?0	00000	0010?	?0100	00000	?001?	1?10?
Enyaliodes laticeps	0000?	V0110	0000V	0000?	V0100	00000	?00?1	0?000
E. oshaughnessyi	0000?	10110	00000	0000?	001?0	00000	?00?1	0?000
E. praestabilis	?????	?????	?????	?????	?????	?????	?????	?????
Hoplocercidae	0000?	10110	00000	0000?	00100	00000	?00?1	0?000
Brachylophus fasciatus	00001	00110	00000	0010?	V0000	00000	?0111	V?101
Dipsosaurus dorsalis	V0001	000V0	V0000	0000?	?0000	00000	?0001	0?000
Iguanidae	00001	00?10	00000	00?0?	?0000	00000	?0??1	0??00
Chalaradon madagascariensis	0000?	000V0	1V100	0VV0?	V0010	00000	?0001	0?000
Oplurus cuvieri	0000?	00110	10100	0000?	100?0	10010	?0001	0?000
O. cyclurus	?????	?????	?????	?????	?????	?????	?????	????0
O. fierinensis	0000?	00010	10000	0000?	00110	01100	?0?1?	1??00
O. quadrimaculatus	0000?	00??0	10100	00???	?00?0	00000	?10??	??000
O. saxicola	?????	?????	?????	?????	?????	?????	?????	????0
Opluridae	0000?	00?10	10?00	0000?	?0?10	???00	??0?1	??000
Callisaurus draconoides	?????	?????	????0	?????	?????	?????	???01	0?000
Petrosaurus mearnsi	1000?	00000	01V01	0V00?	10111	00001	?0?10	0?000
P. repens	?????	?????	?????	?????	?????	?????	?????	?????
P. thalassinus	0000?	00010	00V00	0V00?	1101?	0000?	?0?11	0?000
Phrynosoma asio	0001?	?00?0	10100	0000?	00010	V0100	?0?00	1?001
P. coronatum	0000?	00010	10100	0000?	10011	010?0	?0?0?	??001
P. ditmarsi	?????	?????	?????	?????	?????	?????	?????	???01
P. douglassi	0000?	?0000	00?00	0100?	10011	0VV00	?0???	??001
P. orbiculare	0000?	00010	10100	0100?	1001?	00V?0	?0???	??001
Uma exsul	0001?	00000	00101	0000?	10010	00000	?0?11	V??00
U. inornata	0001?	00000	0010V	0V00?	10010	0V000	?0?11	0?000

APPENDIX 3—*Extended*

44444 12345	44445 67890	55555 12345	55556 67890	66666 12345	66667 67890	77777 12345	77778 67890	88888 12345	88889 67890	99999 12345	999 678
??0??	?????	?????	?????	?????	?????	?????	?????	?????	0????	?????	???
??0??	?????	?????	?????	?????	?????	?????	?????	?????	0????	?????	???
100?0	00???	?????	?????	?????	?????	?????	?????	?????	0????	?????	???
1?0??	??101	00?00	??0??	????0	00??0	00???	00?0?	?????	0????	?????	???
?00?V	00000	00??1	000?0	0?000	00??0	00???	00?0?	??0??	0????	?????	???
1?0?1	00???	?????	????0	???0?	?????	?0???	0????	??0??	0?0??	?????	???
100?V	V011?	00??0	100??	??000	00??0	00???	00?0?	??0??	0?0??	?????	???
?01?0	10V11	00?01	V00??	????0	00??0	00???	00?0?	??0??	??0??	?????	???
??1??	??011	00?01	000??	????0	00??0	00???	00?0?	??0??	??0??	?????	???
??1??	??111	00?01	000??	????0	00??0	00???	0????	??0??	??0??	?????	???
??1?0	?0???	?????	?????	?????	?????	?????	?????	?????	??0??	?????	???
??1??	??1?1	00001	?00??	????0	00??0	00???	00?0?	?00??	??0??	?????	???
?01?0	10111	00?01	000??	????0	00??0	00???	01?0?	??0??	??0??	?????	???
??1??	??101	00001	000??	????0	00??0	00???	0?00?	??0??	??0??	?????	???
??1??	??111	00?01	000??	????0	00??0	?0???	00?0?	??0??	??0??	?????	???
??1?0	10011	00?01	000??	????0	00??0	00???	00?0?	??0??	??0??	?????	???
??1??	??101	00001	000??	????0	00??0	?0???	00?0?	??0??	??0??	?????	???
??1??	??111	00?01	100??	????0	00??0	?0???	00?0?	?????	??0??	?????	???
??1??	??V11	00?01	000??	????0	00??0	?0???	00?0?	??0??	??0??	?????	???
100?0	00??1	0000?	?00?0	0?000	00??0	00???	00?0?	??0??	000??	?????	???
000?1	00???	?????	????0	??0??	?????	?0???	0????	?????	000??	?????	???
000?1	00111	0????	000??	?0000	00??0	00???	00???	??0??	000??	?????	???
000?1	00011	0???0	000?0	?0000	00??0	?0???	00???	??0??	000??	?????	???
0?0?0	00101	0???V	000?1	??000	00??0	00???	00???	??0??	0?0??	?????	???
010?V	00011	0????	?00??	??000	00??0	?0???	00???	??0??	0?0??	?????	???
0?0??	00V01	0???1	?00??	??000	00??0	?0???	00???	??0??	0?0??	?????	???
0?0?V	00001	0???0	?00??	??000	00??0	00???	00???	??0??	0?0??	?????	???
000?1	00011	0???0	000??	??000	00??0	?0???	00???	??0??	0?0??	?????	???
000?1	00?11	0???0	000??	?0000	00??0	00???	00???	??0??	000??	?????	???
00000	00101	V010V	?00?1	????0	00??0	00???	00?0?	??0??	0????	?????	???
00000	00111	00?01	?00??	????0	00??0	?0???	00?0?	??0??	?????	?????	???
0?0??	??111	00?01	?00??	????0	00??0	?0???	00?0?	??0??	?????	?????	???
00000	001?1	0010?	?00?1	????0	00??0	00???	00?0?	??0??	?????	?????	???
00000	0000?	0000?	?00?0	0?000	00??0	?0???	0??0?	??0??	000??	?????	???
00000	V0110	00001	?01?0	00000	00?00	00???	00?0?	??0??	000??	?????	???
00000	00??0	0000?	?0??0	00000	00??0	00???	00?0?	??0??	000??	?????	???
00000	0001V	0??00	001?0	????0	00??0	00???	00???	??0??	?0???	?????	???
00000	100V0	0??01	001??	??0?0	00??0	?1???	00???	??0??	?????	?????	???
0?0??	??011	0??00	?01??	??0?0	00??0	?1???	00???	??0??	?????	?????	???
0?0??	??01V	0??0V	001??	????0	10??0	?0???	00???	??0??	?????	?????	???
000?0	?0010	0??0?	00???	??0?0	00??0	?0???	00???	??0??	?????	?????	???
0?0??	??010	0??00	?01??	????0	00???	00???	00???	??0??	?????	?????	???
00000	?001?	0??0?	001?0	??0?0	?0??0	0????	00???	??0??	?0???	?????	???
?0000	01???	?????	????0	00000	00?10	00???	00?0?	??0??	000??	?????	???
0?000	10?10	10000	000?0	00000	00?00	00???	00?0?	??0??	100??	?????	???
?????	??010	10000	?00?0	?0000	00?10	?1???	01?0?	??0??	1?0??	?????	???
0?000	10010	10000	000?0	?00?0	00?10	01???	01?0?	?00??	1?0??	?????	???
?0000	00?01	00?00	?00??	??0?0	00??0	00???	00?0?	??0??	0????	?????	???
??000	00101	00?00	100?1	00000	00?00	00???	00?0?	??0??	0?0??	?????	???
??0??	???01	00?00	000??	00000	00??0	00???	00?0?	??0??	1????	?????	???
?0000	00?01	00000	000?1	00000	00?00	00???	00?0?	??0??	0?0??	?????	???
?0010	00???	?????	??0?1	??0?0	00???	00???	00?0?	??0??	?????	?????	???
00000	11?00	00000	000?0	??0?0	00?00	00???	01?0?	??0??	000??	?????	???
0000V	11110	0000V	000?0	00000	00?00	00???	00?0?	??0??	000??	?????	???

APPENDIX 3—*Continued*

		1	11111	11112	22222	22223	33333	33334
	12345	67890	12345	67890	12345	67890	12345	67890
U. notata	0001?	00010	00101	0000?	10010	00000	?0?V1	0??00
U. scoparia	0001?	00010	?010V	0V00?	10010	00000	?0?11	0?000
Urosaurus auriculatus	000??	00010	10000	0?00?	1?01?	11000	?0???	??000
U. bicarinatus	?????	?????	?????	?????	?????	?????	?????	???00
U. clarionensis	?????	?????	?????	?????	?????	?????	?????	???00
Uta nolascensis	?????	?????	?????	?????	?????	?????	?????	???00
U. palmeri	?????	?????	?????	?????	?????	?????	?????	???00
U. squamata	?????	?????	?????	?????	?????	?????	?????	???00
U. stansburiana	V000?	00000	00101	0V00?	V1010	00000	?0?00	1?000
Phrynosomatidae	0000?	00000	0010?	0?00?	1?010	00000	?0??0	??000
Anisolepis grilli	0000?	00000	?0000	0000?	0110?	01000	?00??	??001
Chamaeleolis chamaeleonides	?????	?????	?????	?????	?????	?????	?????	????1
C. porcus	?????	?????	?????	?????	?????	?????	?????	????1
Enyalius bilineatus	0000?	00010	00000	0010?	0010?	00000	?V0??	1?101
E. boulengeri	0000?	00000	00100	0000?	0010?	00000	?00??	??100
E. brasiliensis	0000?	00010	01100	0110?	1000?	00000	?1???	0?000
C. catenatus	0000?	?0010	?0100	0?10?	0010?	00000	?10??	??000
E. iheringii	0000?	10010	00100	0010?	1010?	00000	?001?	??001
E. perditus	0000?	00010	?0100	0000?	0010?	00000	?10??	??000
E. pictus	0000?	?0??0	?1100	0????	?010?	00?00	?10??	??000
Phenacosaurus heterodermis	?????	?????	?????	?????	?????	?????	?????	????1
P. richteri	?????	?????	?????	?????	?????	?????	?????	????1
Polychrus acutirostris	0001?	00110	?0000	0100?	VV01?	010V0	?00??	??001
P. femoralis	?????	?????	?????	?????	???1?	?????	?????	???01
P. guttarosus	?????	?????	?????	?????	???1?	?????	?????	???01
P. liogaster	?????	?????	?????	?????	???1?	?????	?????	???01
P. marmoratus	000V?	00110	00000	0100?	V001?	01000	?0001	0?101
Pristidactylus casuhatiensis	0000?	?0011	00010	00?1?	1110?	01000	?0???	???00
P. torquatus	000V?	00110	0V010	??11?	1110?	01000	?V001	0?000
Urostrophus vautieri	0000?	00?10	01000	0010?	0100?	01000	?1???	???01
Polychrotidae	000??	00?10	00000	0??0?	?1???	01000	?10?1	0?00?
Ctenoblepharys adspersus	0010?	00010	00?00	0V00?	1100?	00000	?0???	??000
Leiocephalus carinatus	0010?	00100	0V?00	0V00?	11010	00000	?00??	??000
L. greenwayi	0000?	00000	00?00	0100?	0?010	00000	?0???	??0?0
L. inaguae	?????	?????	?????	?????	?????	?????	?????	????0
L. macropus	001V?	?0000	?0?00	?000?	0V010	0V000	?0?01	0?0?0
L. melanochlorus	0010?	00100	01?00	0100?	00010	00000	?0???	??0?0
L. pratensis	?????	?????	?????	?????	?????	?????	?????	???00
L. psammodromus	0000?	00000	00?00	0000?	0?010	00000	?00??	??0?0
L. schreibersi	0VV0?	00100	00?00	0V00?	00010	00000	?0?11	0???0
Microlophus duncanensis	?000?	00000	?0100	0?0??	00010	00000	?0???	????0
M. grayi	0111?	00??0	00?0?	010??	?101?	10000	?0???	??0?0
M. stolzmanni	?????	?????	?????	?????	?????	?????	?????	???00
M. theresioides	?????	?????	?????	?????	?????	?????	?????	???00
M. tigris	?????	?????	?????	?????	?????	?????	?????	???00
Phymaturus palluma	V000?	00010	0V?00	0V00?	00000	00000	?0000	1?000
P. patagonicus patagonicus	00V0?	000V0	?0?00	0000?	V0000	10000	?0?10	1?000
P. p. payuniae	00VV?	0000V	00?00	0000?	0V000	10000	?0?00	1?000
P. p. somuncurensis	00V0?	000?0	00?00	0V00?	V0000	10000	?0?00	1?000
P. p. zapalensis	0V00?	00000	00?00	0V00?	VV000	10000	?0??0	1?000
P. punae	V000?	00010	01?00	0100?	?0000	V0000	?00?0	1?000
P. sp.	?????	?????	?????	?????	?????	?????	?????	???00
Plesiomicrolophus koepckeorum	?????	?????	?????	?????	?????	?????	?????	????0
Stenocercus guentheri	?????	?????	?????	?????	?????	?????	?????	????0
Uranoscodon superciliosus	000V?	V0010	00000	0V00?	00V1V	00000	?0101	0?V00
Tropiduridae	00?0?	000?0	00?00	0?00?	??0?0	00000	?00??	??000

APPENDIX 3—*Extended—Continued*

44444 12345	44445 67890	55555 12345	55556 67890	66666 12345	66667 67890	77777 12345	77778 67890	88888 12345	88889 67890	99999 12345	999 678
00000	V1?10	00000	000?0	00000	00?00	00???	00?0?	??0??	000??	?????	???
01000	11110	0000V	000?0	00000	00?00	00???	01?0?	?10??	000??	?????	???
??0?0	10010	00000	V00??	??0?0	00???	?0???	00?0?	??0??	?????	?????	???
??0??	??V10	00000	V00??	????0	00??0	?0???	00?0?	??0??	0????	?????	???
??0??	??010	00000	000??	??0?0	00?1?	?1???	00?0?	??0??	1????	?????	???
??0??	???10	?0000	000?0	?0000	00?10	00???	01?0?	??1??	0?0??	?????	???
??0??	??V10	V0000	V01?0	00000	00??0	00???	00?0?	??1??	V00??	?????	???
??0??	??V10	V0000	101?0	00000	00?10	00???	00?0?	??1??	000??	?????	???
?0???	10010	V0000	V00?0	00000	00?10	00???	00?0?	??1??	V00??	?????	???
00000	?0??0	?0000	000?0	00000	00??0	00???	00?0?	??0??	?00??	?????	???
001?0	10010	0??00	?00?1	??0?0	00??0	10???	00???	??0??	0????	?????	???
0?0??	??1V1	0????	000?0	??0?0	00??0	10???	00???	??0??	0????	?????	???
0?0??	??001	0????	?00?1	??0?0	00??0	10???	00???	??0??	0????	?????	???
001?0	10010	0???0	000?1	????0	00??0	00???	00???	??0??	0????	?????	???
001?0	10011	0???0	?00?1	????0	00??0	00???	0????	?????	0????	?????	???
001?1	00011	0??00	000??	????0	00??0	00???	00???	??0??	0????	?????	???
0?1?0	?0011	0??00	?00??	????0	00??0	?0???	0????	?????	0????	?????	???
001?0	10011	0???0	?00??	????0	00??0	00???	01???	??1??	0????	?????	???
001?0	?0011	0???0	?00??	????0	00??0	00???	0????	?????	0????	?????	???
001?0	00011	0????	?00??	????0	00??0	00???	00???	??0??	0????	?????	???
0?0??	??01?	0????	?00?0	??0?0	00??0	10???	00???	??0??	0????	?????	???
0?0??	??01?	0????	?00?0	????0	00??0	?0???	00???	??0??	0????	?????	???
000?0	V0101	00000	000??	????0	00??0	10???	00?0?	??0??	0????	?????	???
0?0??	??111	000?0	?00??	????0	00?10	?0???	00?0?	??0??	0????	?????	???
0?0??	??011	0000?	?00??	????0	00??0	00???	00?0?	??0??	0????	?????	???
0?0??	??011	000??	?00??	????0	00??0	00???	00?0?	??0??	0????	?????	???
000?0	V0011	0000?	000?1	????0	00??0	10???	00?0?	??0??	0????	?????	???
001?0	10???	?????	?????	?????	?????	?????	?????	?????	?????	?????	???
001?0	00110	0??00	000?0	??0?0	00?10	00???	00???	??0??	0?0??	?????	???
001?0	00011	0??00	000?1	??0?0	00??0	10???	00???	??0??	0????	?????	???
00??0	?0???	00000	000??	??0?0	00??0	?????	00?0?	??0??	00???	?????	???
000?1	00001	0??0?	000?0	??0?0	00?10	00???	00???	??0??	0????	?????	???
00000	10?10	0??00	100?0	??0?0	00??0	00???	00???	??0??	00???	?????	???
0?0??	?????	?????	?????	??0??	?0???	?????	0????	?????	0????	?????	???
0?0??	??010	0??0?	000?0	??0?0	00??0	?0???	00???	?10??	0????	?????	???
0?000	10V10	0??0?	?00?0	??0?0	00?10	?0???	00???	??1??	0????	?????	???
0?000	10010	0??0?	V00?0	??0?0	00??0	?0???	00???	?10??	0????	?????	???
0?0??	??V10	0??0?	?0??0	????0	00??0	?0???	00???	??0??	0????	?????	???
0?0??	?0010	0??0?	V00?0	??0?0	00??0	?0???	00???	??0??	0????	?????	???
00000	00010	0??00	100?0	??0?0	00?00	00???	00???	?10??	0????	?????	???
001?1	00???	?????	????0	????0	00??0	?0???	00???	??0??	?????	?????	???
001?1	?0???	?????	????1	????0	00??0	?0???	00???	??0??	?????	?????	???
0?1??	??010	V??0V	?00?0	??0?0	00?00	?0???	00???	?00??	0????	?????	???
0?1??	??010	V??01	000??	????0	00?10	?0???	00???	?10??	?????	?????	???
0?1??	??01V	V??01	000??	??0?0	00?00	?0???	00???	??0??	1????	?????	???
10010	10101	0??0?	000??	??0?0	00??0	00???	00???	??0??	1?0??	?????	???
10010	100V0	0??01	000??	??0?0	00??0	?0???	00???	??0??	1?0??	?????	???
10010	100V0	0??01	000?0	??0?0	00??0	00???	00???	??0??	1?0??	?????	???
10010	100V0	0??01	000??	??0?0	00??0	00???	00???	??0??	1?0??	?????	???
10010	100V0	0??01	000??	??0?0	00??0	00???	00???	??0??	1?0??	?????	???
10010	10101	0??0?	000??	??0?0	00??0	00???	00???	??0??	1?0??	?????	???
1?0??	??0V0	0???1	000??	????0	00??0	?0???	00???	??0??	1????	?????	???
0?1??	??010	V??0?	?00?0	??0?0	00?00	?0???	00???	?10??	1????	?????	???
0?1??	??010	0??0?	001??	????0	00??0	?0???	0????	?????	?????	?????	???
00100	V0001	0??00	?00??	??0?0	00??0	00???	00???	??0??	0????	?????	???
000?0	?00??	0??0?	000?0	??0?0	00??0	00???	00???	?10??	000??	?????	???

APPENDIX 4

Step Matrices for Manhattan Distance Frequency Approach

Given below are the step matrices employed in the coding of character 31 (number of premaxillary teeth) and in the reanalysis of the Montanucci et al. (1975) allozyme data set using the Manhattan distance frequency approach (Wiens, 1995). Each step matrix is labeled by enzyme and given in the same sequence as presented in Montanucci et al. (1975). Only ten of the 27 original allozyme loci held informative character state changes. The ten included loci are coded as characters 89–98 in the data matrix given in Appendix B. The matrix presented at the bottom of the appendix gives the character "states" that were incorporated into the actual data matrix (Appendix B).

31. Number of Premaxillary Teeth:

1	2	3	4	5	6	7	8	9	10	11	12	13
0	22	35	35	48	65	36	39	14	69	69	38	51
22	0	18	18	70	87	54	60	25	82	87	60	69
35	18	0	0	83	100	72	73	43	100	100	73	82
35	18	0	0	83	100	72	73	43	100	100	73	82
48	70	83	83	0	17	16	15	62	39	39	12	22
65	87	100	100	17	0	33	26	79	25	25	27	25
36	54	72	72	16	33	0	15	46	43	48	16	30
39	60	73	73	15	26	15	0	53	33	33	1	15
14	25	43	43	62	79	46	53	0	72	79	52	61
69	82	100	100	39	25	43	33	72	0	20	32	20
69	87	100	100	39	25	48	33	79	20	0	32	18
38	60	73	73	12	27	16	1	52	32	32	0	14
51	69	82	82	22	25	30	15	61	20	18	14	0

(Note: 1: *Gambelia silus*, 2: *G. wislizenii*, 3: *G. copei*, 4: *G. corona*, 5: *Crotaphytus reticulatus*, 6: *C. antiquus*, 7: *C. collaris*, 8: *C. nebrius*, 9: *C. dickersonae*, 10: *C. grismeri*, 11: *C. insularis*, 12: *C. bicinctores*, 13: *C. vestigium*)

	1	2	3	4	5	6	7
89. H-LDH	0	100	100	100	100	100	100
	100	0	100	100	0	0	100
	100	100	0	25	100	100	25
	100	100	25	0	100	100	0
	100	0	100	100	0	0	100
	100	0	100	100	0	0	100
	100	100	25	0	100	100	0
90. a-GPD	0	0	0	0	0	8	17
	0	0	0	0	0	8	17
	0	0	0	0	0	8	17
	0	0	0	0	0	8	17
	0	0	0	0	0	8	17
	8	8	8	8	8	0	8
	17	17	17	17	17	8	0
91. 6-GPD	0	12	0	12	31	5	12
	12	0	12	0	31	7	0
	0	12	0	12	31	5	12
	12	0	12	0	31	7	0
	31	31	31	31	0	31	31
	5	7	5	7	31	0	7
	12	0	12	0	31	7	0
92. ICDs	0	100	0	0	27	29	0
	100	0	100	100	100	100	100
	0	100	0	0	27	29	0
	0	100	0	0	27	29	0
	27	100	27	27	0	17	27
	29	100	29	29	17	0	29
	0	100	0	0	27	29	0
93. ICDm	0	15	0	0	11	19	0
	15	0	15	15	15	11	15
	0	15	0	0	11	19	0
	0	15	0	0	11	19	0

APPENDIX 4—*Continued*

	1	2	3	4	5	6	7
	11	15	11	11	0	13	11
	19	11	19	19	13	0	19
	0	15	0	0	11	19	0
94. GOTs	0	69	100	100	69	69	69
	69	0	100	100	0	0	0
	100	100	0	0	100	100	100
	100	100	0	0	100	100	100
	69	0	100	100	0	0	0
	69	0	100	100	0	0	0
	69	0	100	100	0	0	0
95. Pro	0	56	25	4	15	62	58
	56	0	81	53	41	6	2
	25	81	0	29	40	88	83
	4	53	29	0	11	59	55
	15	41	40	11	0	48	43
	62	6	88	59	48	0	4
	58	2	83	55	43	4	0
96. EST1	0	100	0	80	30	71	100
	100	0	100	40	70	43	33
	0	100	0	80	30	71	100
	80	40	80	0	50	9	20
	30	70	30	50	0	41	70
	71	43	71	9	41	0	29
	100	33	100	20	70	29	0
97. Hbpf	0	7	0	8	0	0	50
	7	0	7	2	7	7	43
	0	7	0	8	0	0	50
	8	2	8	0	8	8	42
	0	7	0	8	0	0	50
	0	7	0	8	0	0	50
	50	43	50	42	50	50	0
98. Tr	0	100	100	100	100	100	100
	100	0	61	100	61	39	61
	100	61	0	100	0	100	0
	100	100	100	0	100	100	100
	100	61	0	100	0	100	0
	100	39	100	100	100	0	100
	100	61	0	100	0	100	0
G. wislizenii	1111111111						
C. dickersonae	2222222222						
C. vestigium	3333333333						
C. bicinctores	4444444444						
C. nebrius	5555555555						
C. collaris	6666666666						
C. reticulatus	7777777777						

Appendix 5

Character Transformations for Each Stem of the Single Most Parsimonious Tree

Characters 1–27, 29–30, 32–67, 69–74, 76–83, 86–88 with a maximum of 24 steps; characters 28, 68, 75, and 84–85 with a maximum of one step; characters 31 and 89–98 with a maximum of 100 steps. PAUP does not calculate consistency indices for characters coded using step matrices. Therefore, "n/a" appears in the CI column for characters 89–98 (allozyme characters coding using Manhattan distances in step matrices). Arrows with double lines indicate unambiguous changes, i.e., those occurring in all optimizations. Arrows with single lines indicate changes that do not occur in all optimizations.

(ACCTRAN optimization):

Branch	Character	Steps	CI	Change
HYPANC → node A	2	1	0.774	a ↔ b
	4	24	1.000	a ⇔ y
	6	24	1.000	a ⇔ y
	10	23	0.462	a ⇔ x
	14	24	1.000	a ⇔ y
	26	2	0.453	a ⇔ c
	29	24	1.000	a ⇔ y
	32	16	0.429	a ⇔ q
	40	4	0.774	a ↔ e
	42	10	0.585	a ⇔ k
	43	24	0.750	a ⇔ y
	45	24	0.247	a ⇔ y
	58	24	0.500	a ↔ y
	71	24	0.500	a ⇔ y
node A ⇉ node B	1	5	0.421	a → f
	2	23	0.774	b ⇉ y
	7	2	0.889	a → c
	12	24	0.727	a ⇉ y
	15	12	1.000	a ⇉ m
	17	19	0.462	e → x
	21	24	1.000	a → y
	24	20	0.857	c → w
	25	24	1.000	a → y
	26	22	0.462	c ⇉ y
	30	24	1.000	a ⇉ y
	36	24	0.632	a ⇉ y
	41	20	0.960	a ⇉ u
	44	24	0.436	a ⇉ y
	46	24	0.800	a → y
	52	24	1.000	a ⇉ y
	55	24	1.000	a → y
	62	24	1.000	a ⇉ y
	82	24	1.000	a → y
node B ⇉ node C	5	24	1.000	a ⇉ y
	11	24	1.000	a → y
	15	12	1.000	m → y
	20	24	1.000	y ⇉ a
	24	2	0.857	w → y
	31	35	n/a	A ⇉ C
	32	6	0.444	q ⇉ w
	41	3	0.960	u → x
	42	5	0.585	k → f
	53	24	1.000	a → y
	60	24	1.000	a → y
	87	24	1.000	a → y
node C ⇉ node D	1	19	0.421	f ⇉ y
node D ⇉ *G. copei*	7	22	0.889	c ⇉ y
	10	1	0.462	x ⇉ y
	12	9	0.727	y ⇉ p
	17	1	0.462	x ⇉ y
	40	3	0.774	e ⇉ h
	41	1	0.960	x ⇉ y
	42	2	0.585	f ⇉ d
node D ⇉ *G. wislizenii*	17	1	0.462	x → w
	31	18	n/a	C ⇉ B
	32	1	0.444	w → v
	36	8	0.632	y → q
	45	22	0.247	y ⇉ c
node C ⇉ *G. coronat*†	1	5	0.421	f → a
	7	2	0.889	c → a
	22	24	0.490	a ⇉ y
	32	2	0.444	w ⇉ y
node B ⇉ *G. silus*	7	1	0.889	c ⇉ d
	10	21	0.462	x → c
	32	3	0.444	q → n
	38	20	1.000	a ⇉ u
	40	4	0.774	e → a
	64	24	0.500	a ⇉ y
node A ⇉ node E	8	24	1.000	a → y
	9	24	1.000	a → y
	10	1	0.462	x ⇉ y
	13	24	1.000	a → y
	19	24	1.000	a ⇉ y
	22	24	0.490	a ⇉ y
	23	24	1.000	a → y
	27	24	1.000	a ⇉ y
	28	1	1.000	0 → 1
	31	38	n/a	A → L
	33	24	1.000	a ⇉ y
	34	24	0.800	a → y
	35	24	1.000	a → y
	37	24	1.000	a → y
	40	20	0.774	e ⇉ y
	42	12	0.585	k ⇉ w
	47	21	0.649	a ⇉ v
	49	24	1.000	a → y
	50	24	1.000	a → y
	54	24	1.000	a ⇉ y
	56	24	1.000	a → y
	57	24	1.000	a ⇉ y
	59	24	1.000	a → y
	61	24	1.000	a ⇉ y
	66	24	1.000	a ⇉ y
	68	1	0.800	0 → 1
	72	24	1.000	a ⇉ y
	76	19	0.558	a ⇉ t
	85	1	1.250	0 → 1
	88	24	1.000	a ⇉ y
	89	100	n/a	1 → 2
	90	8	n/a	1 → 6
	91	12	n/a	1 → 2
	94	69	n/a	1 → 2

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	95	58	n/a	1 → 7
	96	71	n/a	1 → 6
	98	100	n/a	1 → 3
node E ⇉ node F	24	1	0.857	c ⇉ b
	31	1	n/a	L ⇉ H
	45	16	0.247	y → i
	51	2	0.889	a ⇉ e
	68	1	0.800	1 → 2
	69	24	1.000	a ⇉ y
	70	7	0.393	a ⇉ h
	77	7	1.000	a ⇉ h
	85	1	1.250	1 → 4
	86	24	1.000	a ⇉ y
node F ⇉ node G	17	4	0.462	e ⇉ a
	24	1	0.857	b → a
	26	1	0.462	c ⇉ b
	32	2	0.444	q ⇉ s
	42	2	0.585	w ⇉ y
	47	3	0.649	v ⇉ y
	51	20	0.889	e ⇉ y
	70	17	0.393	h ⇉ y
	77	17	1.000	h ⇉ y
	90	8	n/a	6 → 1
	95	43	n/a	7 → 5
node G ⇉ node H	2	1	0.774	b → a
	76	13	0.558	t ⇉ g
node H ⇉ node I	31	1	n/a	H ⇉ L
	39	24	1.000	a ⇉ y
	65	24	1.000	a ⇉ y
	75	1	1.000	0 → 1
	76	6	0.558	g ⇉ a
	78	24	1.000	a ⇉ y
node I ⇉ node J	1	1	0.421	a ⇉ b
	32	8	0.444	s ⇉ k
	44	3	0.436	a ⇉ d
	71	24	0.500	y ⇉ a
	75	1	1.000	1 → 2
	89	100	n/a	2 → 3
	94	100	n/a	2 → 3
	95	11	n/a	5 → 4
node J ⇉ node K	45	4	0.247	i ⇉ e
	70	13	0.393	y → 1
	83	18	0.465	a ⇉ s
node K ⇉ *C. bicinctores*	3	1	0.649	a ⇉ b
	41	1	0.960	a ⇉ b
	51	3	0.889	y ⇉ v
	67	24	0.500	a ⇉ y
	89	25	n/a	3 → 4
	96	9	n/a	6 ⇉ 4
	97	8	n/a	1 ⇉ 4
	98	100	n/a	3 ⇉ 4
node K ⇉ node L	16	9	1.000	a ⇉ j
	26	5	0.462	b ⇉ g
	31	14	n/a	L ⇉ M
	45	2	0.247	e ⇉ c
	68	1	0.800	2 → 3
	73	24	0.500	a ⇉ y

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	75	1	1.000	2 ⇉ 3
	84	1	1.000	0 ⇉ 1
	91	12	n/a	2 → 1
	95	29	n/a	4 → 3
	96	71	n/a	6 → 1
node L ⇉ *C. insularis*	1	23	0.421	b ⇉ y
	16	15	1.000	j ⇉ y
	26	18	0.462	g ⇉ y
	31	18	n/a	M ⇉ K
	32	10	0.444	k ⇉ a
	44	2	0.436	d ⇉ f
	45	2	0.247	c ⇉ a
	47	9	0.649	y ⇉ p
	68	1	0.800	3 → 4
	70	11	0.393	1 ⇉ a
	83	3	0.465	s → p
node L ⇉ *C. vestigium*	24	1	0.857	a ⇉ b
	42	1	0.585	y → x
	70	13	0.393	1 → y
	83	2	0.465	s ⇉ u
node J ⇉ *C. grismeri*	1	4	0.421	b ⇉ f
	17	10	0.462	a ⇉ k
	26	1	0.462	b ⇉ a
	31	32	n/a	L ⇉ J
	42	4	0.585	y ⇉ u
	44	2	0.436	d ⇉ f
	45	7	0.247	i ⇉ p
node I ⇉ *C. dickersonae*	3	24	0.649	a ⇉ y
	18	24	1.000	a ⇉ y
	26	2	0.462	b ⇉ d
	31	52	n/a	L ⇉ I
	48	24	1.000	a ⇉ y
	63	24	1.000	a ⇉ y
	84	1	1.000	0 ⇉ 3
	85	1	1.250	4 ⇉ 3
	92	100	n/a	1 ⇉ 2
	93	15	n/a	1 ⇉ 2
	95	41	n/a	5 → 2
	96	43	n/a	6 ⇉ 2
	97	7	n/a	1 ⇉ 2
	98	61	n/a	3 ⇉ 2
node H ⇉ *C. nebrius*	24	3	0.857	a ⇉ d
	42	1	0.585	y → x
	45	8	0.247	i ⇉ a
	47	2	0.649	y → w
	80	24	0.500	y ⇉ a
	81	23	1.000	a ⇉ x
	83	18	0.465	a ⇉ s
	84	1	1.000	0 ⇉ 2
	85	1	1.250	4 ⇉ 2
	91	31	n/a	2 ⇉ 5
	92	27	n/a	1 ⇉ 5
	93	11	n/a	1 ⇉ 5
	96	41	n/a	6 ⇉ 5
node H ⇉ *C. collaris*	17	17	0.462	e → v
	22	1	0.490	y → x
	31	15	n/a	H ⇉ G

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	32	6	0.444	q ⇉ k
	42	4	0.585	w → s
	45	8	0.247	i ⇉ a
	46	6	0.800	a → g
	47	2	0.649	v → t
	74	24	1.000	y ⇉ a
	80	24	0.500	y ⇉ a
	83	2	0.465	a ⇉ c
	91	7	n/a	2 → 6
	92	29	n/a	1 ⇉ 6
	93	19	n/a	1 ⇉ 6
	95	4	n/a	7 ⇉ 6
	98	100	n/a	3 ⇉ 6
node F ⇉ *C. antiquus*	2	5	0.774	b ⇉ g
	3	12	0.649	a ⇉ m
	10	6	0.462	y ⇉ s
	26	1	0.462	b ⇉ a
	31	26	n/a	H ⇉ F
	34	6	0.800	y ⇉ s
	36	6	0.632	a ⇉ g
	44	24	0.436	a ⇉ y
	45	4	0.247	i → m
	64	24	0.500	a ⇉ y
	67	24	0.500	a ⇉ y
	68	1	0.800	2 → 1
	76	5	0.558	t ⇉ y
	79	24	0.500	a ⇉ y
node E ⇉ *C. reticulatus*	2	1	0.774	b → a
	28	1	1.000	1 → 2
	31	12	n/a	L ⇉ E
	43	8	0.750	y → q
	58	24	0.500	y → a
	73	24	0.500	a → y
	79	24	0.500	a ⇉ y
	89	100	n/a	2 → 7
	90	8	n/a	6 ⇉ 7
	96	29	n/a	6 ⇉ 7
	97	50	n/a	1 ⇉ 7

(DELTRAN optimization):

Branch	Character	Steps	CI	Change
HYPANC ⇉ node A	4	24	1.000	a ↔ y
	6	24	1.000	a ⇔ y
	10	2	0.462	a ↔ c
	14	24	1.000	a ⇉ y
	26	2	0.462	a ↔ c
	29	24	1.000	a ⇔ y
	32	13	0.444	a ⇔ n
	42	5	0.585	a ⇔ f
	43	16	0.750	a ↔ q
	45	8	0.247	a ↔ i
	71	24	0.500	a ⇔ y
node A ⇉ node B	2	24	0.774	a ⇉ y
	12	24	0.727	a ⇉ y
	15	12	1.000	a ⇉ m
	17	18	0.462	e → w
	21	24	1.000	a → y
	24	20	0.857	c → w
	26	22	0.462	c ⇉ y
	30	24	1.000	a ⇉ y
	36	16	0.632	a ⇉ q
	41	20	0.960	a ⇉ u
	43	8	0.750	q → y
	44	24	0.436	a ⇉ y
	46	24	0.800	a → y
	52	24	1.000	a ⇉ y
	55	24	1.000	a → y
	58	24	0.500	a → y
	62	24	1.000	a ⇉ y
	82	24	1.000	a → y
node B ⇉ node C	5	24	1.000	a ⇉ y
	20	24	1.000	y ⇉ a
	25	24	1.000	a → y
	31	35	n/a	A ⇉ C
	32	8	0.444	n ⇉ v
node C ⇉ node D	1	24	0.421	a ⇉ y
	7	2	0.889	a → c
	10	21	0.462	c → x
	11	24	1.000	a → y
	15	12	1.000	m → y
	24	2	0.857	w → y
	40	4	0.774	a → e
	41	3	0.960	u → x
	53	24	1.000	a → y
	60	24	1.000	a → y
node D ⇉ *G. copei*	7	22	0.889	c ⇉ y
	10	1	0.462	x ⇉ y
	12	9	0.727	y ⇉ p
	17	2	0.462	w ⇉ y
	32	1	0.444	v → w
	36	8	0.632	q → y
	40	3	0.774	e ⇉ h
	41	1	0.960	x ⇉ y
	42	2	0.585	f ⇉ d
	45	16	0.247	i → y
node D ⇉ *G. wislizenii*	31	18	n/a	C ⇉ B
	45	6	0.247	i ⇉ c
	87	24	1.000	a → y
node C ⇉ *G. corona*†	22	24	0.490	a ⇉ y
	32	3	0.444	v ⇉ y
node B ⇉ *G. silus*	1	5	0.421	a → f
	7	3	0.889	a ⇉ d
	17	1	0.462	w → x
	36	8	0.632	q → y
	38	20	1.000	a ⇉ u
	42	5	0.585	f → k
	45	16	0.247	i → y
	64	24	0.500	a ⇉ y
node A ⇉ node E	8	24	1.000	a → y
	9	24	1.000	a → y
	10	22	0.462	c ⇉ y
	13	24	1.000	a → y
	19	24	1.000	a ⇉ y
	22	23	0.490	a ⇉ x
	23	24	1.000	a → y
	27	24	1.000	a ⇉ y

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	31	38	n/a	A → L
	33	24	1.000	a ⇉ y
	34	24	0.800	a → y
	35	24	1.000	a → y
	37	24	1.000	a → y
	40	24	0.774	a ⇉ y
	42	13	0.585	f ⇉ s
	47	19	0.649	a ⇉ t
	49	24	1.000	a → y
	50	24	1.000	a → y
	54	24	1.000	a ⇉ y
	56	24	1.000	a → y
	57	24	1.000	a ⇉ y
	59	24	1.000	a → y
	61	24	1.000	a ⇉ y
	66	24	1.000	a ⇉ y
	72	24	1.000	a ⇉ y
	76	19	0.558	a ⇉ t
	88	24	1.000	a ⇉ y
	90	8	n/a	1 → 6
	91	5	n/a	1 → 6
	94	69	n/a	1 → 2
	95	56	n/a	1 → 2
	96	71	n/a	1 → 6
	98	100	n/a	1 → 3
node E ⇉ node F	24	1	0.857	c ⇉ b
	28	1	1.000	0 → 1
	31	1	n/a	L ⇉ H
	43	8	0.750	q → y
	51	4	0.889	a ⇉ e
	58	24	0.500	a → y
	68	1	0.800	0 → 2
	69	24	1.000	a ⇉ y
	70	7	0.393	a ⇉ h
	77	7	1.000	a ⇉ h
	85	1	1.250	0 → 4
	86	24	1.000	a ⇉ y
	89	100	n/a	1 → 2
node F ⇉ node G	17	4	0.462	e ⇉ a
	22	1	0.490	x → y
	26	1	0.462	c ⇉ b
	32	5	0.444	n ⇉ s
	42	5	0.585	s ⇉ x
	47	3	0.649	t ⇉ w
	51	20	0.889	e ⇉ y
	70	17	0.393	h ⇉ y
	77	17	1.000	h ⇉ y
node G ⇉ node H	76	13	0.558	t ⇉ g
	90	8	n/a	6 → 1
node H ⇉ node I	24	1	0.857	b → a
	31	1	n/a	H ⇉ L
	39	24	1.000	a ⇉ y
	47	2	0.649	w → y
	65	24	1.000	a ⇉ y
	76	6	0.558	g ⇉ a
	78	24	1.000	a ⇉ y
node I ⇉ node J	1	1	0.421	a ⇉ b
	32	8	0.444	s ⇉ k
	44	3	0.436	a ⇉ d
	71	24	0.500	y ⇉ a
	75	1	1.000	0 → 2
	95	41	n/a	2 → 5
node J ⇉ node K	45	4	0.247	i ⇉ e
	83	15	0.465	a ⇉ p
	89	100	n/a	2 → 3
	94	100	n/a	2 → 3
	95	11	n/a	5 → 4
node K ⇉ *C. bicinctores*	3	1	0.649	a ⇉ b
	41	1	0.960	a ⇉ b
	42	1	0.585	x → y
	51	3	0.889	y ⇉ v
	67	24	0.500	a ⇉ y
	70	13	0.393	y → l
	83	3	0.465	p → s
	89	25	n/a	3 → 4
	91	7	n/a	6 → 4
	96	9	n/a	6 ⇉ 4
	97	8	n/a	1 ⇉ 4
	98	100	n/a	3 ⇉ 4
node K ⇉ node L	16	9	1.000	a ⇉ j
	26	5	0.462	b ⇉ g
	31	14	n/a	L ⇉ M
	45	2	0.247	e ⇉ c
	73	24	0.500	a ⇉ y
	75	1	1.000	2 ⇉ 3
	84	1	1.000	0 ⇉ 1
node L ⇉ *C. insularis*	1	23	0.421	b ⇉ y
	16	15	1.000	j ⇉ y
	26	18	0.462	g ⇉ y
	31	18	n/a	M ⇉ K
	32	10	0.444	k ⇉ a
	42	1	0.585	x → y
	44	2	0.436	d ⇉ f
	45	2	0.247	c ⇉ a
	47	9	0.649	y ⇉ p
	68	1	0.800	2 → 4
	70	24	0.393	y ⇉ a
node L ⇉ *C. vestigium*	24	1	0.857	a ⇉ b
	68	1	0.800	2 → 3
	83	5	0.465	p ⇉ u
	91	5	n/a	6 → 3
	95	29	n/a	4 → 3
	96	71	n/a	6 → 3
node J ⇉ *C. grismeri*	1	4	0.421	b ⇉ f
	17	10	0.462	a ⇉ k
	26	1	0.462	b ⇉ a
	31	32	n/a	L ⇉ J
	42	3	0.585	x ⇉ u
	44	2	0.436	d ⇉ f
	45	7	0.247	i ⇉ p
node I ⇉ *C. dickersonae*	3	24	0.649	a ⇉ y
	18	24	1.000	a ⇉ y
	26	2	0.462	b ⇉ d
	31	52	n/a	L ⇉ I
	42	1	0.585	x → y
	48	24	1.000	a ⇉ y

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	63	24	1.000	a ⇉ y
	75	1	1.000	0 → 1
	84	1	1.000	0 ⇉ 3
	85	1	1.250	4 ⇉ 3
	91	7	n/a	6 → 2
	92	100	n/a	1 ⇉ 2
	93	15	n/a	1 ⇉ 2
	96	43	n/a	6 ⇉ 2
	97	7	n/a	1 ⇉ 2
	98	61	n/a	3 ⇉ 2
node H ⇉ *C. nebrius*	24	2	0.857	b ⇉ d
	45	8	0.247	i ⇉ a
	80	24	0.500	y ⇉ a
	81	23	1.000	a ⇉ x
	83	18	0.465	a ⇉ s
	84	1	1.000	0 ⇉ 2
	85	1	1.250	4 ⇉ 2
	91	31	n/a	6 ⇉ 5
	92	27	n/a	1 ⇉ 5
	93	11	n/a	1 ⇉ 5
	95	41	n/a	2 → 5
	96	41	n/a	6 ⇉ 5
node H ⇉ *C. collaris*	2	1	0.774	a → b
	17	17	0.462	e → v
	31	15	n/a	H ⇉ G
	32	3	0.444	n ⇉ k
	45	8	0.247	i ⇉ a
	46	6	0.800	a → g
	74	24	1.000	y ⇉ a
	80	24	0.500	y ⇉ a
	83	2	0.465	a ⇉ c
	92	29	n/a	1 ⇉ 6
	93	19	n/a	1 ⇉ 6
	95	6	n/a	2 ⇉ 6
	98	100	n/a	3 ⇉ 6
node F ⇉ *C. antiquus*	2	6	0.774	a ⇉ g
	3	12	0.649	a ⇉ m
	10	6	0.462	y ⇉ s
	24	1	0.857	b → a
	26	1	0.462	b ⇉ a
	31	26	n/a	H ⇉ F
	34	6	0.800	y ⇉ s
	36	6	0.632	a ⇉ g
	42	1	0.585	x → y
	44	24	0.436	a ⇉ y
	45	4	0.247	i → m
	47	2	0.649	w → y
	64	24	0.500	a ⇉ y
	67	24	0.500	a ⇉ y
	68	1	0.800	2 → 1
	76	5	0.558	t ⇉ y
	79	24	0.500	a ⇉ y
node E ⇉ *C. reticulatus*	22	1	0.490	x → y
	28	1	1.000	0 → 2
	31	12	n/a	L ⇉ E
	32	3	0.444	n → q
	42	4	0.585	s → w
	45	16	0.247	i → y

APPENDIX 5—*Continued*

Branch	Character	Steps	CI	Change
	47	2	0.649	t → v
	68	1	0.800	0 → 1
	73	24	0.500	a → y
	79	24	0.500	a ⇉ y
	85	1	1.250	0 → 1
	89	100	n/a	1 → 7
	90	8	n/a	6 ⇉ 7
	91	7	n/a	6 → 7
	95	2	n/a	2 → 7
	96	29	n/a	6 ⇉ 7
	97	50	n/a	1 ⇉ 7

APPENDIX 6

List of Character State Changes by Character

Characters 1–27, 29–30, 32–67, 69–74, 76–83, 86–88 with a maximum of 24 steps; characters 28, 68, 75, and 84–85 with a maximum of one step; characters 31 and 89–98 with a maximum of 100 steps. PAUP does not calculate consistency indices for characters coded using step matrices. Therefore, "n/a" appears in the CI column for characters 89–98 (allozyme characters coding using Manhattan distances in step matrices). Arrows with double lines indicate unambiguous changes, i.e., those occurring in all optimizations. Arrows with single lines indicate changes that do not occur in all optimizations.

(ACCTRAN optimization):
Character change lists:

Character	CI	Steps	Changes
1	0.421	5	node A a → f node B
		19	node C f ⇉ y node D
		5	node C f → a *G. coronat*†
		1	node I a ⇉ b node J
		23	node L b ⇉ y *C. insularis*
		4	node J b ⇉ f *C. grismeri*
2	0.774	1	node A b ↔ a HYPANC
		23	node A b ⇉ y node B
		1	node G b → a node H
		5	node G b ⇉ g *C. antiquus*
		1	node E b → a *C. reticulatus*
3	0.649	1	node K a ⇉ b *C. bicinctores*
		24	node I a ⇉ y *C. dickersonae*
		12	node G a ⇉ m *C. antiquus*
4	1.000	24	node A y ⇔ a HYPANC
5	1.000	24	node B a ⇉ y node C
6	1.000	24	node A y ⇔ a HYPANC
7	0.889	2	node A a → c node B
		22	node D c ⇉ y *G. copei*
		2	node C c → a *G. coronat*†
		1	node B c ⇉ d *G. silus*
8	1.000	24	node A a → y node E
9	1.000	24	node A a → y node E
10	0.462	23	node A x ⇔ a HYPANC
		1	node D x ⇉ y *G. copei*
		21	node B x → c *G. silus*
		1	node A x ⇉ y node E
		6	node G y ⇉ s *C. antiquus*
11	1.000	24	node B a → y node C
12	0.727	24	node A a ⇉ y node B
		9	node D y ⇉ p *G. copei*
13	1.000	24	node A a → y node E
14	1.000	24	node A y ⇔ a HYPANC
15	1.000	12	node A a ⇉ m node B
		12	node B m → y node C
16	1.000	9	node K a ⇉ j node L
		15	node L j ⇉ y *C. insularis*
17	0.462	19	node A e → x node B
		1	node D x ⇉ y *G. copei*
		1	node D x → w *G. wislizenii*
		4	node F e ⇉ a node G
		10	node J a ⇉ k *C. grismeri*
		17	node F e → v *C. collaris*
18	1.000	24	node I a ⇉ y *C. dickersonae*
19	1.000	24	node A a ⇉ y node E
20	1.000	24	node B y ⇉ a node C
21	1.000	24	node A a → y node B
22	0.490	24	node C a ⇉ y *G. coronat*†
		24	node A a ⇉ y node E
		1	node F y → x *C. collaris*
23	1.000	24	node A a → y node E
24	0.857	20	node A c → w node B
		2	node B w → y node C
		1	node E c ⇉ b node F
		1	node F b → a node G
		1	node L a ⇉ b *C. vestigium*
		3	node H a ⇉ d *C. nebrius*
25	1.000	24	node A a → y node B
26	0.462	2	node A c ⇔ a HYPANC
		22	node A c ⇉ y node B
		1	node F c ⇉ b node G
		5	node K b ⇉ g node L
		18	node L g ⇉ y *C. insularis*
		1	node J b ⇉ a *C. grismeri*
		2	node I b ⇉ d *C. dickersonae*
		1	node G b ⇉ a *C. antiquus*
27	1.000	24	node A a ⇉ y node E
28	1.000	1	node A 0 → 1 node E
		1	node E 1 → 2 *C. reticulatus*
29	1.000	24	node A y ⇔ a HYPANC
30	1.000	24	node A a ⇉ y node B
31	n/a	35	node B A ⇉ C node C
		18	node D C ⇉ B *G. wislizenii*
		38	node A A → L node E
		1	node E L ⇉ H node F
		1	node H H ⇉ L node I
		14	node K L ⇉ M node L
		18	node L M ⇉ K *C. insularis*
		32	node J L ⇉ J *C. grismeri*
		52	node I L ⇉ I *C. dickersonae*
		26	node G H ⇉ F *C. antiquus*
		15	node F H ⇉ G *C. collaris*
		12	node E L ⇉ E *C. reticulatus*
32	0.444	16	node A q ⇔ a HYPANC
		6	node B q ⇉ w node C
		1	node D w → v *G. wislizenii*
		2	node C w ⇉ y *G. coronat*†
		3	node B q → n *G. silus*
		2	node F q ⇉ s node G
		8	node I s ⇉ k node J
		10	node L k ⇉ a *C. insularis*
		6	node F q ⇉ k *C. collaris*
33	1.000	24	node A a ⇉ y node E
34	0.800	24	node A a → y node E
		6	node G y ⇉ s *C. antiquus*
35	1.000	24	node A a → y node E
36	0.632	24	node A a ⇉ y node B
		8	node D y → q *G. wislizenii*
		6	node G a ⇉ g *C. antiquus*
37	1.000	24	node A a → y node E
38	1.000	20	node B a ⇉ u *G. Silus*
39	1.000	24	node H a ⇉ y node I
40	0.774	4	node A e ↔ a HYPANC
		3	node D e ⇉ h *G. copei*

APPENDIX 6—*Continued*

Character change lists:			
Character	CI	Steps	Changes
		15	node F H ⇉ G *C. collaris*
		12	node E L ⇉ E *C. reticulatus*
32	0.444	13	node A n ⇔ a HYPANC
		8	node B n ⇉ v node C
		1	node D v → w *G. copei*
		3	node C v ⇉ y *G. coronat*†
		5	node F n ⇉ s node G
		8	node I s ⇉ k node J
		10	node L k ⇉ a *C. insularis*
		3	node F n ⇉ k *C. collaris*
		3	node E n → q *C. reticulatus*
33	1.000	24	node A a ⇉ y node E
34	0.800	24	node A a → y node E
		6	node G y ⇉ s *C. antiquus*
35	1.000	24	node A a → y node E
36	0.632	16	node A a ⇉ q node B
		8	node D q → y *G. copei*
		8	node B q → y *G. silus*
		6	node G a ⇉ g *C. antiquus*
37	1.000	24	node A a → y node E
38	1.000	20	node B a ⇉ u *G. silus*
39	1.000	24	node H a ⇉ y node I
40	0.774	4	node C a → e node D
		3	node D e ⇉ h *G. copei*
		24	node A a ⇉ y node E
41	0.960	20	node A a ⇉ u node B
		3	node C u → x node D
		1	node D x ⇉ y *G. copei*
		1	node K a ⇉ b *C. bicinctores*
42	0.585	5	node A f ⇔ a HYPANC
		2	node D f ⇉ d *G. copei*
		5	node B f → k *G. silus*
		13	node A f ⇉ s node E
		5	node F s ⇉ x node G
		1	node K x → y *C. bicinctores*
		1	node L x → y *C. insularis*
		3	node J x ⇉ u *C. grismeri*
		1	node I x → y *C. dickersonae*
		1	node G x → y *C. antiquus*
		4	node E s → w *C. reticulatus*
43	0.750	16	node A q ← a HYPANC
		8	node A q → y node B
		8	node E q → y node F
44	0.436	24	node A a ⇉ y node B
		3	node I a ⇉ d node J
		2	node L d ⇉ f *C. insularis*
		2	node J d ⇉ f *C. grismeri*
		24	node G a ⇉ y *C. antiquus*
45	0.247	8	node A i ← a HYPANC
		16	node D i → y *G. copei*
		6	noe D i ⇉ c *G. wislizenii*
		16	node B i → y *G. silus*
		4	node J i ⇉ e node K
		2	node K e ⇉ c node L
		2	node L c ⇉ a *C. insularis*
		7	node J i ⇉ p *C. grismeri*
		8	noe H i ⇉ a *C. nebrius*
		4	node G i → m *C. antiquus*
		8	node F i ⇉ a *C. collaris*
		16	node E i → y *C. reticulatus*
46	0.800	24	node A a → y node B
		6	node F a → g *C. collaris*
47	0.649	19	node A a ⇉ t node E
		3	node F t ⇉ w node G
		2	node H w → y node I
		9	node L y ⇉ p *C. insularis*
		2	node G w → y *C. antiquus*
		2	node E t → v *C. reticulatus*
48	1.000	24	node I a ⇉ y *C. dickersonae*
49	1.000	24	node A a → y node E
50	1.000	24	node A a → y node E
51	0.889	4	node E a ⇉ e node F
		20	node F e ⇉ y node G
		3	node K y ⇉ v *C. bicinctores*
52	1.000	24	node A a ⇉ y node B
53	1.000	24	node C a → y node D
54	1.000	24	node A a ⇉ y node E
55	1.000	24	node A a → y node B
56	1.000	24	node A a → y node E
57	1.000	24	node A a ⇉ y node E
58	0.500	24	node A a → y node B
		24	node E a → y node F
59	1.000	24	node A a → y node E
60	1.000	24	node C a → y node D
61	1.000	24	node A a ⇉ y node E
62	1.000	24	node A a ⇉ y node B
63	1.000	24	node I a ⇉ y *C. dickersonae*
64	0.500	24	node B a ⇉ y *G. silus*
		24	node G a ⇉ y *C. antiquus*
65	1.000	24	node H a ⇉ y node I
66	1.000	24	node A a ⇉ y node E
67	0.500	24	node K a ⇉ y *C. bicinctores*
		24	node G a ⇉ y *C. antiquus*
68	0.800	1	node E 0 → 2 node F
		1	node L 2 → 4 *C. insularis*
		1	node L 2 → 3 *C. vestigium*
		1	node G 2 → 1 *C. antiquus*
		1	node E 0 → 1 *C. reticulatus*
69	1.000	24	node E a ⇉ y node F
70	0.393	7	node E a ⇉ h node F
		17	node F h ⇉ y node G
		13	node K y → l *C. bicinctores*
		24	node L y ⇉ a *C. insularis*
71	0.500	24	node A y ⇔ a HYPANC
		24	node I y ⇉ a node J
72	1.000	24	node A a ⇉ y node E
73	0.500	24	node K a ⇉ y node L
		24	node E a → y *C. reticulatus*
74	1.000	24	node F y ⇉ a *C. collaris*
75	1.000	1	node I 0 → 2 node J
		1	node K 2 ⇉ 3 node L
		1	node I 0 → 1 *C. dickersonae*
76	0.558	19	node A a ⇉ t node E
		13	node G t ⇉ g node H
		6	node H g ⇉ a node I
		5	node G t ⇉ y *C. antiquus*

APPENDIX 6—*Continued*

Character change lists:

Character	CI	Steps	Changes
77	1.000	7	node E a ⇉ h node F
		17	node F h ⇉ y node G
78	1.000	24	node H a ⇉ y node I
79	0.500	24	node G a ⇉ y *C. antiquus*
		24	node E a ⇉ y *C. reticulatus*
80	0.500	24	node H y ⇉ a *C. nebrius*
		24	node F y ⇉ a *C. collaris*
81	1.000	23	node H a ⇉ x *C. nebrius*
82	1.000	24	node A a → y node B
83	0.465	15	node J a ⇉ p node K
		3	node K p → s *C. bicinctores*
		5	node L p ⇉ u *C. vestigium*
		18	node H a ⇉ s *C. nebrius*
		2	node F a ⇉ c *C. collaris*
84	1.000	1	node K 0 ⇉ 1 node L
		1	node I 0 ⇉ 3 *C. dickersonae*
		1	node H 0 ⇉ 2 *C. nebrius*
85	1.250	1	node E 0 → 4 node F
		1	node I 4 ⇉ 3 *C. dickersonae*
		1	node H 4 ⇉ 2 *C. nebrius*
		1	node E 0 → 1 *C. reticulatus*
86	1.000	24	node E a ⇉ y node F
87	1.000	24	node D a → y *G. wislizenii*
88	1.000	24	node A a ⇉ y node E
89	n/a	100	node E 1 → 2 node F
		100	node J 2 → 3 node K
		25	node K 3 → 4 *C. bicinctores*
		100	node E 1 → 7 *C. reticulatus*
90	n/a	8	node A 1 → 6 node E
		8	node G 6 → 1 node H
		8	node E 6 ⇉ 7 *C. reticulatus*
91	n/a	5	node A 1 → 6 node E
		7	node K 6 → 4 *C. bicinctores*
		5	node L 6 → 3 *C. vestigium*
		7	node I 6 → 2 *C. dickersonae*
		31	node H 6 ⇉ 5 *C. nebrius*
		7	node E 6 → 7 *C. reticulatus*
92	n/a	100	node I 1 ⇉ 2 *C. dickersonae*
		27	node H 1 ⇉ 5 *C. nebrius*
		29	node F 1 ⇉ 6 *C. collaris*
93	n/a	15	node I 1 ⇉ 2 *C. dickersonae*
		11	node H 1 ⇉ 5 *C. nebrius*
		19	node F 1 ⇉ 6 *C. collaris*
94	n/a	69	node A 1 → 2 node E
		100	node J 2 → 3 node K
95	n/a	56	node A 1 → 2 node E
		41	node I 2 → 5 node J
		11	node J 5 → 4 node K
		29	node L 4 → 3 *C. vestigium*
		41	node H 2 → 5 *C. nebrius*
		6	node F 2 ⇉ 6 *C. collaris*
		2	node E 2 → 7 *C. reticulatus*
96	n/a	71	node A 1 → 6 node E
		9	node K 6 ⇉ 4 *C. bicinctores*
		71	node L 6 → 3 *C. vestigium*
		43	node I 6 ⇉ 2 *C. dickersonae*
		41	node H 6 ⇉ 5 *C. nebrius*
		29	node E 6 ⇉ 7 *C. reticulatus*
97	n/a	8	node K 1 ⇉ 4 *C. bicinctores*
		7	node I 1 ⇉ 2 *C. dickersonae*
		50	node E 1 ⇉ 7 *C. reticulatus*
98	n/a	100	node A 1 → 3 node E
		100	node K 3 ⇉ 4 *C. bicinctores*
		61	node I 3 ⇉ 2 *C. dickersonae*
		100	node F 3 ⇉ 6 *C. collaris*

APPENDIX 7

Scleral Ossicle Data

Scleral ossicle numbers and patterns of overlap were assessed in the listed specimens. All crotaphytids examined match the apparently plesiomorphic iguanian condition in which ossicles 1, 6, and 8 are positive and 4, 7, and 10 are negative (Underwood, 1970; de Queiroz, 1982). Only one set of scleral ossicles (one eye) was examined in the specimens followed by asterisks.

Crotaphytus:	
bicinctores	REE 2931, 2932, 2934
antiquus	TNHC 53155*, 53156, 53159
collaris	REE 2875, 2944, 2952*
dickersonae	REE 2777, 2904, 2905
grismeri	MZFC 6648, 6649, 6650*
insularis	REE 2794–2796
nebrius	REE 2937, 2941, 2942, 2943
reticulatus	REE 2910, 2911, 2913*
vestigium	REE 2820, 2825, 2826
Gambelia:	
copei	REE 2798, 2802, 2804
silus	CAS 22713, 22742*, 141328*
wislizenii	REE 2789*, 2790, 2791, 2792, 2916[1], 2917, 2918[2], 2919, 2920

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[1] Ossicles 1 and 14 of the right scleral ring are partially overlapping.

[2] Ossicles 1 and 14 of the right scleral ring and 13 and 14 of the left ring are partially overlapping.