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UNIVERSITY OF CALIFORNIA, BERKELEY, PH.D, 1978

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The Evolutionary Development of the Texas *Eurycea*

(Amphibia: Plethodontidae)

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The Evolutionary Development of the Texas *Eurycea* (Amphibia: Plethodontidae)

By

Samuel Spender Sweet

B.S. (Cornell University) 1970
M.A. (University of California) 1973

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CHAPTER I

INTRODUCTION

Assemblages of relict populations may comprise natural experiments which can be of central importance in the study of evolutionary mechanisms. Though most of these isolates ultimately disappear through the continued actions of the agencies which initiated their disjunction, their potential to originate novel adaptive solutions is high; dissociated from the mediating genetic influence of their conterminous ancestral populations and under strong selection in a deteriorating environment, these relicts may evolve at a comparatively rapid rate. Irrespective of the eventual outcome, the characteristics of the adaptive process contain information of general relevance. When a number of mutually isolated relicts occur in an area the experiment may be considered to exist in replicated form, with some degree of variation in the experimental conditions provided by the natures of the selective regimes and the capabilities of the responding populations. The results of such evolutionary experiments are potentially interpretable at a useful level of generality, especially when few selective parameters are of overriding importance. Here population responses constitute systems of parallel adaption, whose features reflect the evolutionary mechanisms we seek.

A variety of criteria may be advanced concerning the evaluation of the suitability of an animal group and of an

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environment for investigations of this kind. The existence of relict populations presupposes low vagility; ideally dispersal ability should be less than the distance separating the component populations of the relictual assemblage, for only under these conditions is parallelism the reasonable interpretation for the existence of shared derived characters. The number of replicates available is directly dependent upon the degree of genetic isolation existing among relict populations. The actual number of replicates is of lesser importance, though in general there are advantages in a larger assemblage of relicts. An animal group favorable for this type of analysis should further display some form of variability, either among individuals (polymorphism, etc) or in its life cycle (such as a staged life history); such features may represent coincident adaptations with respect to deteriorating environmental conditions, and may be selectively modified in the relict populations. Finally, the participating populations should be sufficiently closely related at the time of distributional disjunction to permit assumptions of a reasonable degree of genetic homogeneity and a resultant homology of structures as initial conditions.

No less important are the characteristics of the environment in which the relicts occur; ideally the processes of environmental change which fragmented the distribution of an ancestral stock should be ongoing, and should show some

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degree of spatial and temporal consistency. The fewer the modalities of change, and the more deleterious (to a point) their effects vis à vis the adaptedness of the relicts, the better. The point is that strong directional selection engendered by a small number of environmental variables through time provides a better experimental design than does a variable, heterogeneous or episodic selective regime.

The full complement of these criteria approaches satisfaction in relatively few relict assemblages and/or environments. Among the vertebrates such systems may exist, for example, among fishes in the deteriorating drainages of the Great Basin, or in amphibians, reptiles and small mammals in mountainous or mesic environments which have been broadly affected by climatic changes through geologic time. Among the latter, a small group of salamanders now relict on the Edwards Plateau of central Texas is the focus of this work. Their suitability in terms of the criteria here established is considered below.

These salamanders, of the plethodontid genus Eurycea, are separated by a gap of several hundred kilometers from the continuous range of their congeners (Figure 1). They presently occupy restricted spring and cave habitats which are mutually isolated among themselves to the extent that movement of individuals between populations can be reasonably assumed to be highly improbable (Chapters III and IV). Nonetheless, populations occur over a broad area of the Ed-

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Figure 1. The distribution of salamanders of the genus *Eurycea* in eastern and central North America, showing the disjunction between distributions in the Interior Highlands and on the Edwards Plateau.

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wards Plateau and are relatively numerous. These salamanders have a biphasic life history as a primitive condition and the larval and adult stages are both structurally and ecologically distinct. Evidence presented below (Chapters IV, V, VI and VII) indicates that these relict populations of Eurycea share a common ancestry.

The Edwards Plateau of central Texas satisfies the environmental criteria noted above in a manner which provides for the consistent replication of selective regimes among isolated populations of salamanders. The region is a broad, geologically homogeneous limestone uplift, subdivided by drainages and sharply bounded by a geological discontinuity along its dissected edge (Figure 2). Highly restricted mesic environments occur near springs on the plateau, which is otherwise a decidedly xeric region whose western third forms an eastern extension of the Chihuahuan desert. Regional drying trends since the late Tertiary have affected the plateau, balanced by mesic intervals during the Pleistocene, but from the viewpoint of the Texas Eurycea the effective aridity of the habitat has been steadily increasing since the time of distributional disjunction. This is because the erosional processes reducing the plateau bring about the gradual failure of springs (Chapters II and V), and thus the deterioration of mesic conditions within the area accessible to each population. By virtue of the influence of this single geomorphological process most of the

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Figure 2. Geomorphologic subdivisions of central Texas. Outcrop regions of Comanche Series limestones are stippled; the dashed outline encompasses those counties which are here considered to delimit the Edwards Plateau (excluding the Llano Uplift).

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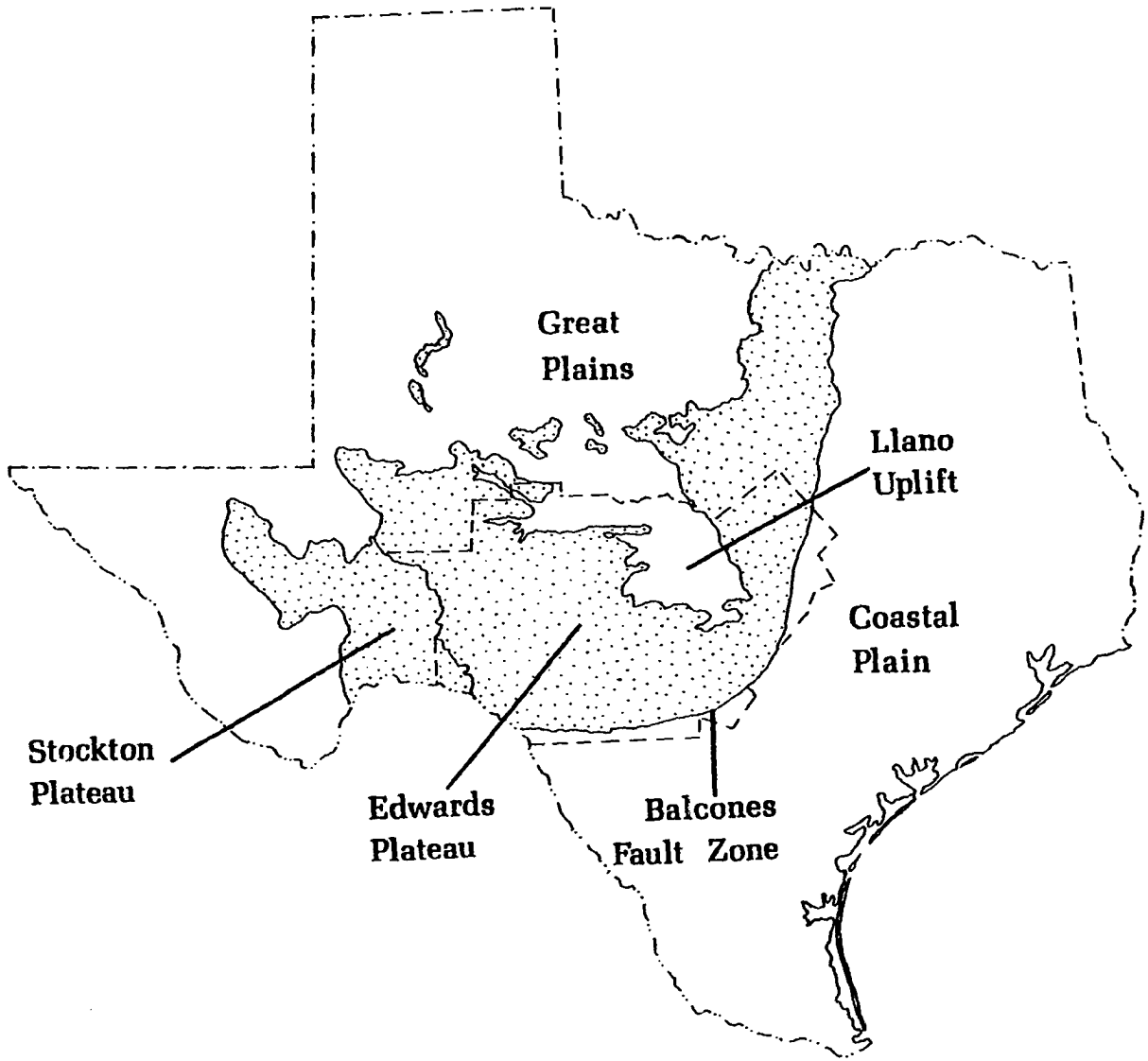

epigean (spring-inhabiting) populations of the Texas Eurycea appear to be under qualitatively similar selective regimes. A smaller number of populations of the Texas Eurycea are troglobitic (cave-inhabiting). The caves of the Edwards Plateau provide stable wet conditions over a much longer period than do individual springs. Being formed by flowing groundwater, cave systems extend and deepen as erosion of the land surface proceeds (see Chapter II); aquatic troglobites may disperse throughout these systems, and face loss of suitable habitat only when the cave forming rocks are entirely eroded away. The selective regimes encountered by populations colonizing caves are thus quite different from those of the epigean environment, but both exhibit strong directionality. The general similarity of adaptations observed in all troglobitic animal groups is evidence for the comparability of selective processes as a characteristic of the cave environment as a whole (see Chapter IV).

Thus the populations of Eurycea which occur as relicts on the Edwards Plateau satisfy all of the criteria established above, and may be argued to constitute a system of replicated natural experiments in adaptation. In the sections below this group is placed in the context of its relationship to other salamanders, the existing literature is reviewed, and the sequence and contents of the investigations comprising this dissertation are detailed.

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Systematic Position of the Texas Eurycea

The Texas Eurycea represent a lineage of generalized lungless salamanders within the family Plethodontidae. The plethodontids comprise the largest and most diverse of the nine modern families of salamanders (Edwards, 1976), containing about 220 described species in 23 genera (Brame, 1967); an additional 20-30 probable new species are known and await description. Plethodontid salamanders are primarily a New World group, with the notable exception of two species of the genus Hydromantes which occur on the Italian peninsula and on Sardinia.

On the whole, plethodontids are chiefly upland and montane salamanders, though a number of species have adapted to the moist eastern coastal plains of North and Central America. Centers of plethodontid diversity are associated with most of the major orogenic regions of the New World, including the Appalachians and the western remnants of the Ouachita structural belt (the Interior Highlands and the Edwards Plateau), the Coast Ranges and Sierra Nevada of western North America, the margins of the Mexican Plateau, and the volcanic and tectonic uplands of Central America and northern South America (Wake, 1966; Wake and Lynch, 1976). Only the Rocky Mountains, Great Basin ranges, and the central and southern Andes show little or no development of plethodontid diversity. Numbers of genera and species, and the overall abundance of individuals remain

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greatest in the southern Appalachians, the probable center of origin of the family (Dunn, 1926; Wake, 1966).

The Plethodontidae contains two sharply defined subfamilies, the Desmognathinae and the Plethodontinae, with the latter clearly separable into three major groups designated as tribes by Wake (1966); these are the tribes Hemidactyliini, Plethodonini, and Bolitoglossini. Desmognathines, hemidactyliines and plethodonines are most numerous in the Appalachians, and occur in the Interior Highlands as well; several hemidactyliines and one plethodonine reach the Edwards Plateau. The plethodonines also occur in western North America, and are most diverse in the Coast Ranges; the center of diversity of the desmognathines and hemidactyliines lies in the Appalachian region. Bolitoglossine plethodontids occur in Italy, the Coast Ranges and Sierra Nevada of western North America, and from the margins of the Mexican Plateau south and east to northern South America, with multiple centers of diversity (Wake and Lynch, 1976).

Hemidactyliine plethodontids include the least derived members of the family; all have a free living aquatic larval stage, and most species are semiaquatic as adults, displaying a mosaic of generalized and specialized features (Wake, 1966). Salamanders of the genus Eurycea are the most diverse of the eight genera of hemidactyliines, representing 14 of the 23 currently recognized species. Six of

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these nominate species occur in the Appalachians, five in the Interior Highlands (two endemics, three shared with the Appalachians) and six on the Edwards Plateau. All of the Appalachian species retain a biphasic life cycle, whereas the endemics of the Interior Highlands and of the Edwards Plateau show tendencies towards the suppression of metamorphosis (Table 1). This condition is termed paedogenesis, following the definition provided by Wake (1966); the term neoteny is partially synonymous but is widely misunderstood, and is avoided here. Gould (1977) has reexamined these concepts, and resurrects the term progenesis for the condition apparently present in sexually mature larval hemidactyliines; I am unconvinced of the value of this rarefaction of inherently analytic terminology for the evolutionary modification of developmental processes and prefer the simple descriptive quality of the term paedogenesis.

Three monotypic genera of troglobitic salamanders apparently share a common ancestry with Eurycea (Wake, 1966) and occur around the periphery of the present distribution of that genus. Typhlotriton spelaeus occurs in the caves of the Ozark Plateau in the Interior Highlands; it is a metamorphosing species less derived in morphology than are the species of Eurycea (Wake, 1976; Brandon, 1970; 1971; Lombard and Wake, 1977). Haideotriton wallacei (Carr, 1939; Valentine, 1964; Brandon, 1967; 1968; 1971) and Typhlomolge rathbuni (Brandon, 1971; Russell, 1976) are paedogenetic

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Table 1. The distribution of life-history patterns among species of *Eurycea* in the three regions of occurrence of the genus. Most species are obligate in metamorphosis (M) or paedogenesis (P); where mixed strategies occur the preponderant mode is indicated first.

Species	Regions of Occurrence		
	Appalachians	Interior Highlands	Edwards Plateau
Eurycea aquatica	M		
E. bislineata	M		
E. junaluska	M		
E. longicauda	M	M	
E. lucifuga	M	M	
E. quadridigitata	M	M	
E. multiplicata		M,P	
E. tynerensis		P	
E. neotenes			P,M
E. nana			P
E. pterophila			P
E. latitans			P
E. troglodytes			P
E. tridentifera			P

species. Haideotriton occurs in caves of the Dougherty Plain of southwestern Georgia and adjacent Florida, and Typhlomolge occurs in caves of the Balcones Fault Zone in a restricted area along the eastern margin of the Edwards Plateau of central Texas. Wake (1966) suggests that the hemidactyliines are presently in a third cycle of distributional expansion and retraction. In this model, Typhlotriton, Haideotriton and Typhlomolge represent relicts of an early Tertiary radiation of salamanders ancestral to the genus Eurycea; the second cycle, perhaps of Miocene age, is represented by the endemic species of Eurycea occupying the Interior Highlands and the Edwards Plateau. The third cycle, probably of Quaternary age, is represented by the species of Eurycea which now occur in both the Appalachian region and the Interior Highlands (Table 1). The time sequence proposed by Wake for the occurrence of hemidactyliine salamanders on the Edwards Plateau has been challenged by Mitchell and Smith (1972), but is supported by the data in Chapter II.

Development of the Literature Concerning the Texas Eurycea

The existence of small aquatic salamanders on the Edwards Plateau was first made known by Stejneger (1896), who described the advanced troglobite Typhlomolge rathbuni from an artesian well in San Marcos, Hays County. Stejneger noted similarities between Typhlomolge and salamanders of the genera Necturus and Proteus, to which he allied the new

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genus in the "superfamily Proteoideae." Stejneger stated that Typhlomolge was a permanently larval salamander noting the presence of large ova in some of his specimens. It remained for Emerson (1905) to demonstrate on the basis of a detailed anatomical investigation that T. rathbuni was a plethodontid, sharing many similarities with larvae of Pseudotriton ruber. This decision was accepted by Dunn (1926) and all subsequent authors.

The discovery of T. rathbuni led to an intense interest in the cave fauna of the San Marcos area, led by Eigenmann (1899; 1900a, b; 1909), Norman (1900) and Uhlenhuth (1919; 1921; 1923). This fact, coupled with a reasonable amount of herpetological survey collecting by Strecker (1908; Strecker and Williams, 1927) and others, makes it somewhat surprising that the widespread and abundant spring-dwelling populations of the Texas Eurycea passed unnoticed (at least in the literature) until the advent of the Wrights in the early 1930's. Neither Strecker nor the professional collector G. W. Marnock seem to have noted these salamanders, though the type series of Eurycea neotenes was subsequently collected a short distance from Marnock's ranch at Helotes, Bexar County (Bishop and Wright, 1937). E. D. Cope visited Marnock in 1877 and spent three weeks on the Edwards Plateau. In a series of letters quoted by Osborn (1931: 234-240) Cope writes of travelling overland from Helotes to Mason, Mason County, across a part of the plateau where epigean popula-

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tions of Eurycea are now abundant. Cope repeatedly noted camping by the springs in the headwater canyons of the Medina, Guadalupe and Llano Rivers, but apparently neither he nor Marnock inspected them closely.

In the course of their extensive field work in central Texas, A. H. and A. A. Wright discovered epigean populations of Eurycea, and located a troglobitic population near Boerne, Kendall County, through Ellen Quillen of the Witte Museum, San Antonio. A specimen from this population, collected in 1933, is in the collection of Cornell University. The Wrights communicated their information to Sherman Bishop (R. T. Clausen, personal communication, 1969) who visited the Helotes area in 1937 and collected the type series of Eurycea neotenes (Bishop and Wright, 1937). Charles E. Mohr collected specimens of the Cascade Caverns population for Bishop in 1940 or 1941, and in the latter year sent him specimens (collected in 1938) from a second epigean population (at San Marcos Springs, Hays County), which Bishop described as Eurycea nana (Bishop, 1941). The existing distributional information was summarized by Wright and Wright (1938) and Bishop (1943).

At about this time B. C. Brown, A. G. Flury and F. E. Potter, Jr. were associated at the University of Texas, Austin, and undertook to collect further material of Eurycea neotenes. Their early work (Brown, 1942; 1950) uncovered

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populations in Kerr and Gillespie Counties; several additional localities were documented by specimens in the Texas Natural History Collection, Austin, but these were not reported for nearly 20 years (Baker, 1961). Both Brown and Potter accumulated large private collections between about 1941 and 1955 whose contents remain unreported. Potter secured a number of specimens from the Cascade Caverns population in 1946 which formed the type series of Eurycea latitans (Smith and Potter, 1946); a fourth species, Eurycea pterophila (Burger, Smith and Potter, 1950), was diagnosed from material collected for comparison with E. latitans. That there was room for confusion in the diagnoses of these species is evidenced by Milstead's (1951) misidentification of a specimen of E. neotenes from an epigean site in Kerr County as E. latitans.

During the late 1950's organized interest arose, again centered around the University of Texas, in a systematic survey of the caves of the Edwards Plateau. Several troglobitic populations were discovered between 1956 and 1960 by J. K. Baker, W. H. Russell, and others. Baker (1957) diagnosed the most advanced troglobitic Eurycea yet discovered, E. troglodytes, from Valdina Farms Sinkhole, Medina County, and began a trend in the interpretation of the adaptations of troglobitic populations which continues to the present time. Baker pointed out that E. troglodytes was intermediate in morphology between epigean populations of Eurycea

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and Typhlomolge rathbuni, but that "this does not imply that Eurycea troglodytes is a 'missing link' between Eurycea and Typhlomolge but only demonstrates a way that Typhlomolge could have evolved from a Eurycea-type ancestor and the way Eurycea does evolve under the influences of a cave environment" (195[illegible], pp. 335-336). Further, after noting that evolution is proceeding in a parallel fashion among troglobitic populations, Baker suggested that the existence of species of Eurycea which approach T. rathbuni in their degree of troglobitic adaptation may indicate a closer relationship between the two genera than was then recognized.

Baker continued his work with the Texas Eurycea, and in 1961 published a distributional account which remains the primary source of information on the epigean populations. This was based on material collected by Baker, Flury and Potter, and by Clark Hubbs and his associates in the course of survey work on the fishes of the Edwards Plateau. Baker added 10 counties to the known range of the Texas Eurycea, providing data for the range cited by Conant (1958); subsequent work has not extended this distribution appreciably. Notable in Baker's account are several records for troglobitic populations in Comal and Kendall Counties, within the known range of epigean populations of the Texas Eurycea, and a single troglobitic population in southern Val Verde County, far to the southwest of the known epigean distribution. Baker expanded the known range of E. latitans from

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Cascade Caverns to the adjacent (and probably linked) Cascade Sinkhole System, and to Deadman's Cave and Century Caverns, a large interconnected system about 10 miles to the north.

Baker was apparently unaware of a population of advanced cave salamanders discovered three years previously (Anon., 1959) at Honey Creek Cave, Comal County. These specimens, collected by W. H. Russell and R. Ballinger, were given to Floyd Potter for description. This population was also located by B. C. Brown in about 1950 (personal communication, 1970); nothing was done with this material, and the population was eventually described as Eurycea tridentifera by Mitchell and Reddell (1965). The morphological gap between troglobitic populations of Eurycea and Typhlomolge rathbuni was greatly reduced by the discovery of E. tridentifera, leading Mitchell and Reddell (1965, p. 23) to place Typhlomolge in the synonymy of Eurycea. Reddell and Mitchell developed an interest in troglobitic populations of Eurycea and undertook to accumulate material from a number of cave populations which had been located by W. H. Russell and others of the Texas Speleological Survey. Reddell summarized this distributional information in two faunal checklists (1967; 1971), adding 13 troglobitic populations to those previously reported. On the basis of this material Reddell and Mitchell decided to describe five additional species of Eurycea (the Salamander Cave, Bender's Cave, Bad-

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weather Pit, Carson Cave and Fourmile Cave populations), but deferred on the project when diagnoses proved difficult (J.R. Reddell, personal communication, 1974).

James P. Bogart (1967) examined karyotypes of a number of epigean and troglobitic populations of the Texas Eurycea and found them superficially very similar; nonetheless, he concluded that species status was warranted for most of the troglobitic populations and for several of the epigean populations.

The generic rearrangement proposed by Mitchell and Reddell (1965) was overturned by Wake (1966). Several skull, vertebral and tarsal characteristics were found to be shared by E. tridentifera and T. rathbuni, but not with E. troglodytes, E. pterophila and E. nana, leading Wake (1966:66) to redefine Typhlomolge as a genus comprised of two species, tridentifera and rathbuni. Mitchell and Smith (1972) presented evidence which they felt refuted Wake's conclusions, but their work was reduced in value by the admixture and confusion of ontogenetic changes in osteology with adult conditions representing varying degrees of troglobitic adaptation. The matter of the generic allocation of tridentifera and rathbuni remains unsettled; authors in Texas have tended to follow Mitchell and Reddell (e.g. Thomas, 1974; Russell, 1976; Longley, 1978), while the majority of herpetologists have accepted Wake's allocation (e.g. Brame, 1967; Brandon, 1971; Raun and Gehlbach, 1972; Gorham, 1974). I

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(Sweet, 1976; 1977 a; b) prefer a third option retaining the allocations of the original authors, as does Conant (1975).

An infrequently cited major paper by Brandon (1971) provides a variety of information on named troglobitic populations of the Texas Eurycea and Typhlomolge, including proportional features and tooth counts. Brandon also examined the reproductive tracts in available material of Eurycea latitans, E. troglodytes, E. tridentifera and T. rathbuni, demonstrating that each of these species is paedogenetic (as had long been assumed). Testis lobation (first reported in the group by Wake [1966]) was shown to be positively correlated with increasing body size.

The remaining literature on the Texas Eurycea is in a broad sense either physiological or ecological in scope, or represents accounts composed of secondary information from the literature. In the last category are checklist accounts by Schmidt (1953), Baker (1966), Brown (1967a;b;c), Raun and Gehlbach (1972), Thomas (1974), and Sweet (1977b). Much of the physiological work with the Texas Eurycea has involved attempts at inducing metamorphosis with exogenous thyroxine treatments (Kezer, 1952; Potter and Rabb, 1960; Dundee, 1957; see also Bogart, 1967). In general this treatment is effective in inducing metamorphosis in E. neotenes and E. nana, but not so in E. tridentifera (Bogart, 1967; Wake, 1966), nor in Typhlomolge rathbuni (Dundee, 1957).

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Reports on oxygen consumption in E. nana, E. pterophila and E. neotenes (Norris, Grandy and Davis, 1963), and on the chemistry of skin pigments in this trio of species (Barrett and Benjamin, 1977) are also in the literature.

There has been scant ecological interest in the Texas Eurycea until rather recently. Hunsaker and Potter (1961) reported "redleg" (Aeromonas spp.) infections in a population of Eurycea neotenes, but did not elaborate on the extent or significance of the apparent epidemic. Bruce (1971; 1976) collected large summer samples from two populations of Eurycea neotenes in Kerr County; finding a heavy preponderance of juveniles, he proposed a model for the evolution of paedogenesis which involved selection for reduced age at first reproduction coupled with an environmentally-determined minimum size for metamorphosed individuals. Sexual maturity is apparently reached early in the second year of life. Nonetheless, Eurycea neotenes does metamorphose in some localities (Sweet, 1977a), and juveniles are less abundant in general than in the populations sampled by Bruce; paedogenesis may be primarily a response to the restricted occurrence of reliable habitat. A thorough but largely descriptive account of the population dynamics of Eurycea nana was recently presented by Tupa and Davis (1976); this species, restricted in occurrence to a single very large spring, reproduces throughout the year. Eurycea neotenes appears to have a long but seasonal egg-deposition period

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during winter and spring, to judge from the broad size range of immature specimens observed in summer collections and evidence from the small number of mature specimens available from the winter months (Bruce, 1976; Sweet, 1977a). The population biology of troglobitic species remains little known; heavily gravid females of Eurycea latitans, E. troglodytes and E. tridentifera have been collected from April through September (Bogart, 1967; Brandon, 1971), and it is possible that reproductive activity is aseasonal. Evidence is emerging that Typhlomolge rathbuni may reproduce throughout the year (Longley, 1978).

Introduction to Present Work

My interest in the Texas Eurycea began in late 1968 as a result of dissatisfaction with the level of information available in the literature. Survey collecting during the summer of 1969 indicated that both surface- and cave-dwelling populations were more numerous and diverse than might have been expected in such a clearly relictual assemblage; accordingly, a more extensive collecting program was carried out during the summers of 1970 and 1971. Much of the material collected in 1971 was used in an attempt to assess the relationships among populations by artificially-induced metamorphosis. The rationale for this work was that while present populations of the Texas Eurycea are divergently specialized, much of this modification probably occurred subsequent to the origin of paedogenesis; thus the metamor-

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phosed adult stage, not expressed and thus not directly exposed to selection, might prove a reliable indicator of the ancestries of populations. This line of inquiry proved intractable with the discovery that relatively few surface-dwelling and no troglobitic populations will undergo morphologically complete metamorphosis under treatment with thyroxine. The metamorphosed adult component of the genome is either strongly influenced by selection for larval adaptations, or has been degraded by the accumulation of mutations since it ceased to be expressed.

Field work was continued in the summers of 1973 and 1974, with an emphasis on locating peripheral epigean populations and building samples from known troglobitic populations. Tissue samples were collected and frozen from a large number of populations; the use of electrophoretic techniques to assess relationships among populations was investigated, but discontinued after survey analyses failed to show the existence of significant diversity within the group (Yanev and Sweet, unpublished data). No unique alleles were noted, though frequency differences apparently exist; the sample sizes necessary to work with these data were not available for many of the critical populations. The tissue samples remain preserved in the Museum of Vertebrate Zoology.

Approximately 3700 specimens were collected and preserved during the course of this work, representing 85 epigean and 19 troglobitic populations. This sample was aug-

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mented by about 700 specimens borrowed from museums and individuals which represent an additional 10-20 epigean and three troglobitic populations, in addition to significantly increasing sample sizes for a number of sites already represented. All of the specimens collected in the course of this work and the field notes concerning them are deposited in the Museum of Vertebrate Zoology.

This dissertation addresses the development of diversity in the Texas Eurycea, with emphasis on the derivation of a comprehensive overview of the evolution of the group. Each chapter save the first is written as a largely independent unit, with references to other chapters inserted where appropriate. While this method of organization results in some redundancy of content, variation in the emphasized aspects of the repeated material reduces literal redundancy to a few introductory remarks. Some familiarity with the preceeding sections is increasingly assumed in later chapters as larger subsets of the material are called upon in abbreviated notation. Figures, tables and appendices are numbered consecutively throughout the work to preclude the possibility of confusion.

The rationale for the sequence and contents of chapters can be briefly explained. Populations of the Texas Eurycea, whether epigean or troglobitic, occupy spatially restricted patches of suitable habitat in a predominantly unfavorable environments; these patches and their characteristics are

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largely determined by the geomorphology of the Edwards Plateau. Thus it is inevitable that regional geology becomes a major factor in this work, and a thorough discussion of the topic is prerequisite to an understanding of the importance of parallel evolution in the Texas Eurycea. There exists no published account sufficient for this purpose in either scope or detail; Chapter II represents this synthesis derived both from the literature and from field observations.

A major part of this investigation has involved the basic documentation of the distribution of populations of the Texas Eurycea. Chapters III (epigean populations) and IV (troglobitic populations) provide this information and some related analyses. Epigean populations are restricted to springs, but were absent from a number of the sites examined; this pattern is examined and explained in terms of regional geomorphology. A general predictive model is derived for the occurrence of epigean populations and the mode of origin of troglobitic populations. In addition to distributional information Chapter IV contains analyses of the evolution of troglobitic adaptations in populations of the Texas Eurycea, and investigates the patterns of morphological similarity affiliating subsets of this sample. Geologic criteria are employed in distinguishing grades of parallel adaptation from monophyletic groups of troglobites.

The discovery of populations of Eurycea neotenes in

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which metamorphosis occurs permits for the first time an examination of the accepted generic allocation of these salamanders, and provides insights into the evolution of paedogenesis in the group; this material constitutes Chapter V.

Evaluation of the systematic status of the various troglobitic populations is a potentially difficult matter. Many of these populations appear to have been independently derived from epigean ancestors, and may be reasonably assumed to be responding to a homogeneous selective regime in the cave environment. The potential for rapid rates of adaptation in a parallel fashion reduces the value of morphological distinctiveness or similarity as evidence of the degree of relatedness among these largely allopatric populations. An instance of sympatry between epigean E. neotenes and an advanced troglobitic population of E. tridentifera is analyzed in Chapter VI; the interaction between these end members of the continuum of troglobitic adaptation provides a baseline against which other populations may be assessed. Individuals of the remaining described troglobitic species (E. latitans and E. troglodytes) display unusual attributes which are shared with some individuals of the sympatric populations, suggesting that they may be influenced by secondary contact as well. Chapter VI evaluates this evidence and provides a new interpretation of the systematic status of these taxa based on the interaction of epigean and trog-

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lobitic populations.

Epigean populations of the Texas Eurycea have been allocated to three species. Single populations comprise E. nana and E. pterophila, with the remaining populations generally assigned to E. neotenes. Chapter VII tests the validity of E. pterophila through an analysis of its supported diagnostic features in comparison to the range of variation displayed by populations of E. neotenes.

The results of this series of investigations are drawn together in the final chapter. The development of diversity in the Texas Eurycea is placed in the context of ongoing erosional dissection of the Edwards Plateau, enabling a synthesis of the evolutionary history of this group of salamanders. The origin of paedogenesis and the process of cave colonization are seen to be components of a general trend of increasing distributional restriction which has as its result the development of an extensive parallel radiation of troglobitic populations. The systematics of the Texas Eurycea is redefined to reflect the implications of this general model.

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CHAPTER II

GEOMORPHOLOGY OF THE EDWARDS PLATEAU

Introduction

Central Texas is a topographically undistinguished region of low relief and rolling character, marked by two major structural features, the Balcones Fault Zone and the Llano Uplift. The low scarp of the Balcones Fault Zone rises in the vicinity of Waco and extends to the southwest through Austin and San Antonio, gradually attaining 100-150 m in relief before turning westward to subside as a topographic feature in the vicinity of Del Rio. The fault zone demarcates the predominantly Cenozoic sediments of the Gulf Coastal Plain from an extensive low plateau of Cretaceous limestones to the north and west, whose continuity is broken only by an elliptical depression surrounding the Llano Uplift. This structural dome consists of a complex of Precambrian rocks with associated blocks of Paleozoic sediments which are locally produced into prominent hills. The southeastern portion of the Cretaceous plateau exclusive of the Llano Uplift constitutes the region known as the Edwards Plateau, and is the area of primary interest in the present work. The eastern and southern boundaries of the Edwards Plateau are sharply demarcated by the Balcones Fault Zone, whereas the northern and western limits are arbitrarily defined. The canyon of the Pecos River is generally accepted as the western border of the Edwards Plateau, dividing it from the structurally similar Stockton Plateau to the west. On the

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north the Edwards Plateau merges evenly into the southern terminus of the Great Plains and no boundary has been consistently recognized. For the purposes of this work the northern margin of the Edwards Plateau is considered to be the northern edges of Crockett, Tom Green, Concho, McCullouch, San Saba, Lampasas and Coryell counties, exclusive of the region of pre-Mesozoic rocks comprising the Llano Uplift. So defined, the Edwards Plateau is consistent with geologic characterizations, and is included within the biogeographic provinces recognized by Blair (1950), Correll and Johnston (1970) and Mitchell and Reddell (1971); the former pair do not exclude the Llano Uplift, and all extend the plateau somewhat farther to the northwest. The major structural features and political subdivisions of the Edwards Plateau are indicated in Figure 3.

The geology, topography and hydrology of the Edwards Plateau are treated in detail in subsequent sections, as a familiarity with the geomorphology of the plateau is necessary for a comprehensive exposition of the factors influencing the distribution and evolutionary history of the Texas Eurycea. A synopsis of this discussion is presented below.

Passing inland from the Balcones Fault Zone the Comanche Series limestones of the plateau surface are flat-lying, modified from their original condition mainly by uplift and erosion. Exposed formations comprise a stratigraphic sequence from upper Trinity Division (Glen Rose Formation) through the Fredericksburg Division (primarily Edwards Group

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Figure 3. Major geomorphological features of the Edwards Plateau. Dashed lines delimit counties (see Fig. 7); the margin of the Balcones Fault Zone and the Llano Uplift are marked by hatchured lines. The major drainages mentioned in the text are indicated, as identified below: a, San Gabriel River; b, Colorado River; c, Pedernales River; d, Llano River; e, Blanco River; f, Guadalupe River; g, Cibolo Creek; h, Medina River; i, Sabinal River; j, Frio River; k, Nueces River; l, West Nueces River; m, Devils River; n, Rio Grande; and o, Pecos River.

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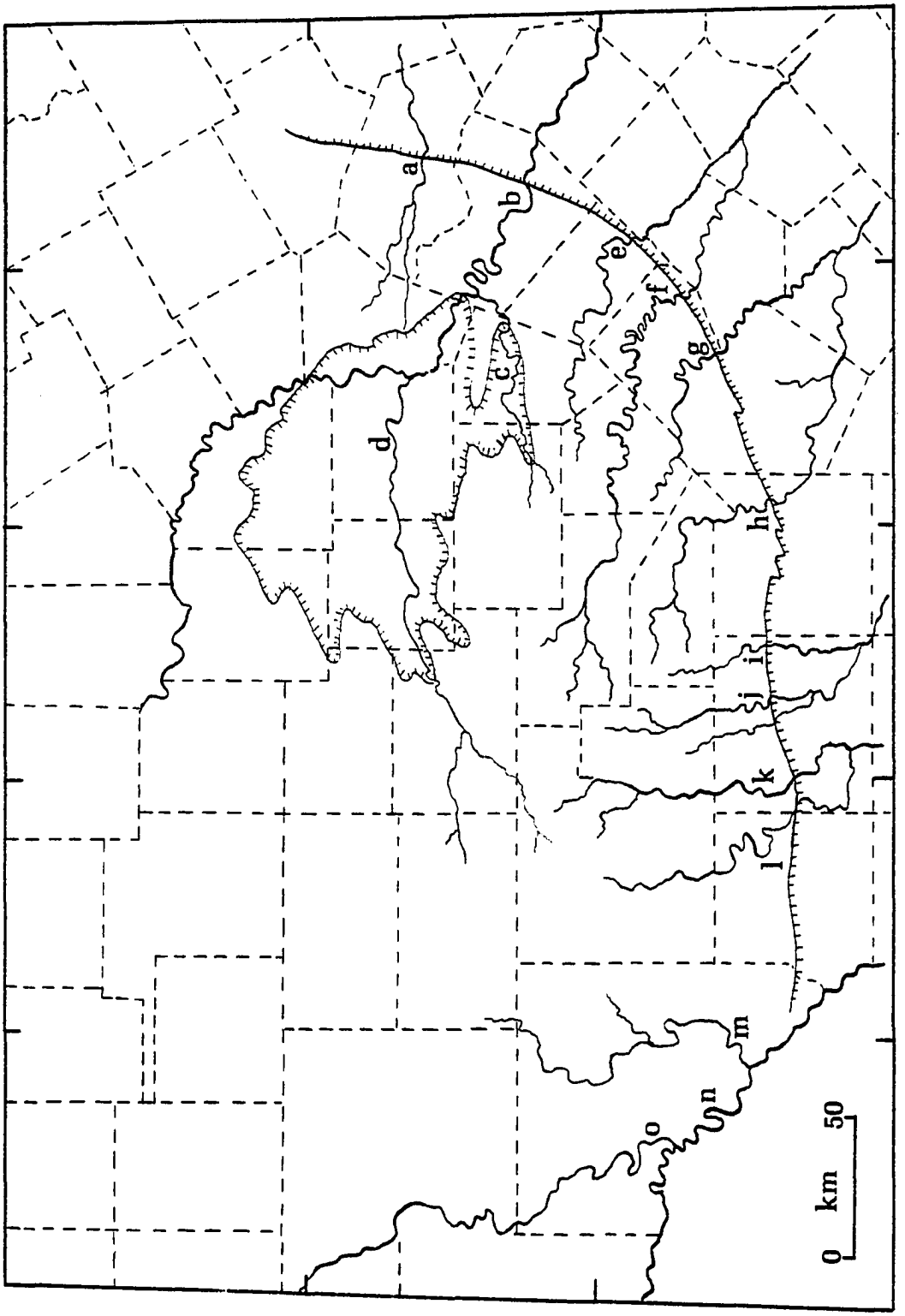

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limestones of the Fort Terrett and Segovia Formations) to the top of the Washita Division (comprised of the Georgetown, Del Rio and Buda Formations). Rocks of the Trinity, Fredericksburg and lower Washita Divisions were deposited during Lower Cretaceous time (Neocomian, Aptian and Albian stages), while those of the Del Rio and Buda Formations were laid down during the Cenomanian Stage of the Upper Cretaceous. The relations among faunal and stratigraphic units in the sediments of the Edwards Plateau are displayed in Table 2. Elevations decrease radially away from a broad upland located in the southwest central region of the plateau, associated with the headwaters of the Colorado, San Antonio, Nueces and Rio Grande basins, with the steepest relief gradients occurring in the drainages of the southern and western margins of the plateau. Canyons here develop 150-200 m in relief, cutting down to upper Trinity Division deposits and resulting in permanent stream flow derived from the subsurface drainage of the plateau proper, where all but the largest streams are intermittent. The extensive erosional dissection of the plateau margin since its elevation in late Tertiary time, together with the characteristics of the fractured and downfaulted Fredericksburg rocks of the Balcones Fault Zone gives rise to a regionally simple (though locally complex) hydrology. This consists of two cycles of recharge, subterranean flow and discharge, and produces a subdivided zone of mesic environments in an otherwise subhumid to semiarid landscape. Precipitation on the plateau surface is conducted underground

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Table 2. Faunal and stratigraphic subdivisions of the Comanche Series limestones of the Edwards Plateau region from the North Texas-Tyler Basin across the San Marcos Platform to the edge of the Maverick Basin (modified from numerous sources).

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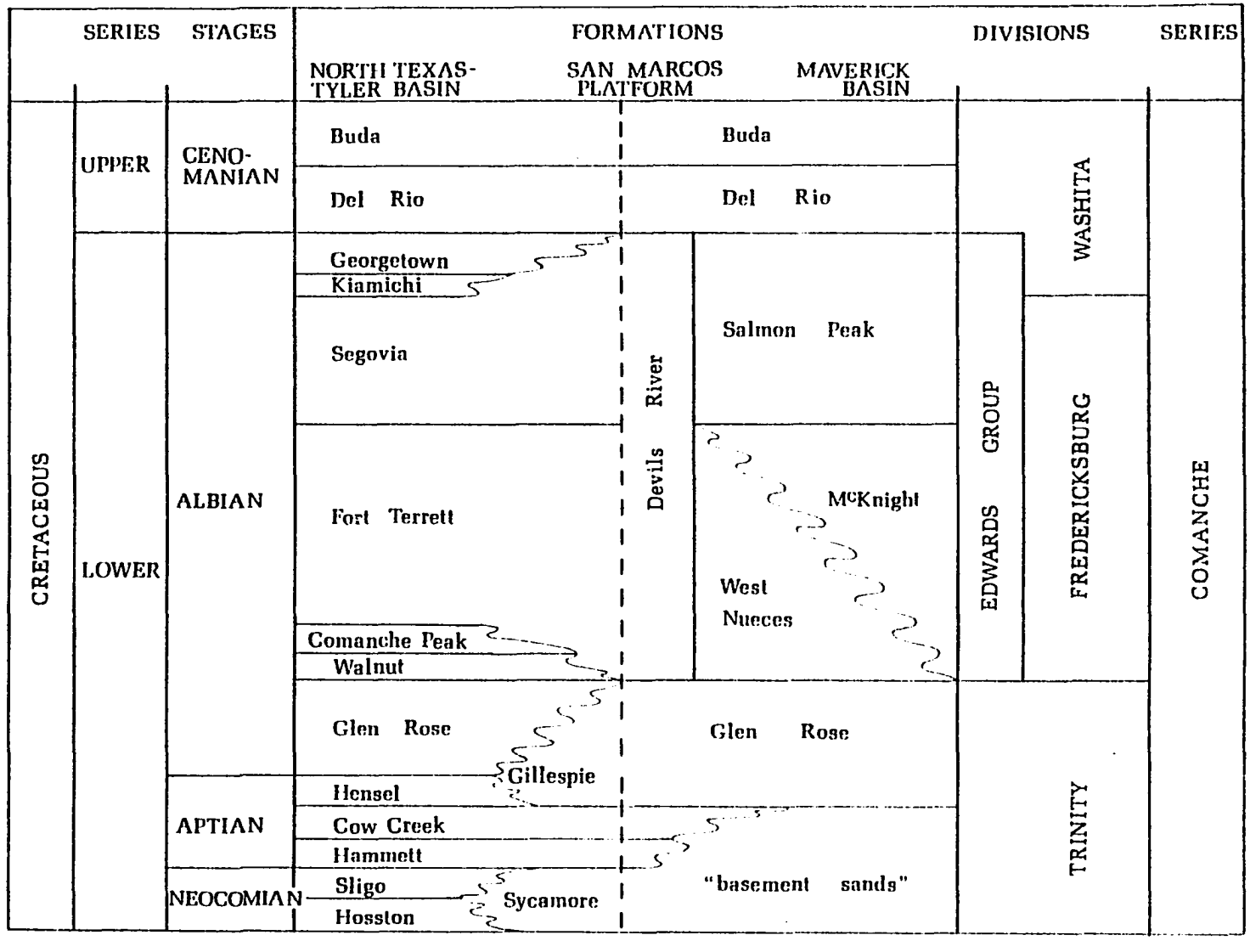

through dolines and fissures and moves gradually southeastward following the regional dip of the strata to emerge in springs in the canyons of the marginal drainages, comprising the base flows of these streams. Most of the flow in these drainages passes into the subsurface in crossing the fractured strata of the Balcones Fault Zone, recharging an extensive water-table and artesian aquifer along the edge of the plateau; this aquifer discharges at a few major springs distributed along the coastal edge of the escarpment. While the topography of the plateau is not markedly karstic, small scale solutional features such as dolines, sinkholes and small caves systems are abundant as a consequence of the extensive development of subterranean drainages. These features are chiefly developed in the lower Glen Rose and lower Fort Terrett Formations, and are influential in the development of diversity in the Texas Eurycea.

Formation and Development of the Edwards Plateau

Basement features

The present form of the Edwards Plateau is in large part determined by the position and structure of the pre-Mesozoic basement rocks; the influence of this foundation is seen in the regional slope and lithologic sequence of the Lower Cretaceous limestones which comprise the body of the plateau (Stricklin, Smith and Lozo, 1971; Rose, 1972), and in the location and structure of the Balcones Fault Zone (King, 1961b). A brief discussion of the basement features of the plateau region is thus useful in understanding subse-

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quent depositional, tectonic and erosional events.

The pre-Mesozoic surface in central Texas is comprised of two major structural units: the Precambrian rocks of the Texas Craton (Flawn, 1956); and the Paleozoic sedimentary and metasedimentary deposits of the Ouachita Structural Belt (Flawn, et al, 1961). The Texas Craton is an extensive, predominantly granitic body whose southeastern periphery is overlain by the Ouachita Belt. In this area the craton is dominated by two structural domes, the Devils River and Llano Uplifts, which approach or reach the present land surface in the Del Rio and Llano regions (Figure 4). The Llano Uplift is much the larger of the two features, and is comprised of middle Precambrian metasedimentary rocks (gneiss and schist) with extensive granitic intrusions (Flawn, 1956); age determinations for the various components of the uplift (reviewed by Clabaugh and McGehee, 1972) range from 850 to 1100 million years. The uplift has roughly 2000 m of relief from the local Precambrian surface, and is separated from the Devils River Uplift to the southwest by the Kerr and Val Verde basins (Flawn, et al, 1961, Plate 4). The Devils River Uplift is a smaller, more abrupt feature apparently largely composed of metavolcanic rocks. It displays about 5000 m of relief from the local Precambrian surface and reaches to within about 800 m of the present land surface (Flawn, 1961g, Fig. 2); the age of its constituents is not known.

The surface structure of the Texas Craton was defined by erosion during late Precambrian and early Cambrian time,

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Figure 4. Basement features of the Edwards Plateau region (modified from Flawn, 1956; 1961).

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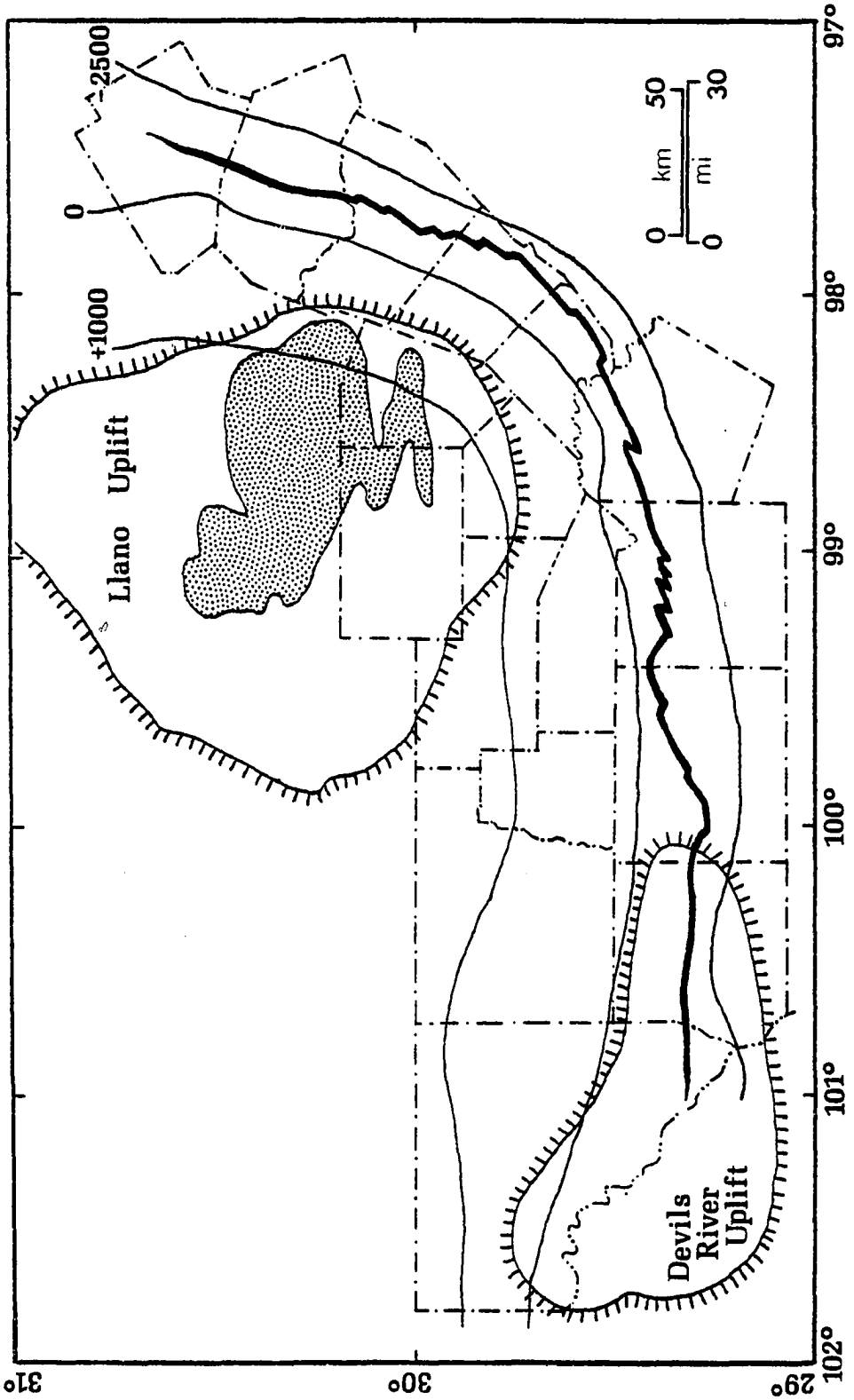

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then gradually buried by sediments during a long Paleozoic inundation (Barnes and Cloud, 1972; Bell, 1972; Bell and Barnes, 1972), broken by the orogenic phase which produced the Ouachita Structural Belt.

The Ouachita system is the remains of a late Paleozoic orogenic sequence associated with the final closure of the proto-Atlantic and the formation of Pangaea. It appears to bear close similarities in structure to other mountain belts produced by continental collisions, including the Appalachians, the Alps and the Himalayas. Like them, the Ouachita system is known or thought to consist of a trio of rather discrete structural zones (Bucher, 1955; Flawn, 1961e; King, 1961a): an inland zone of folded and thrusted sedimentary rocks, partially overridden by a series of highly sheared metasedimentary nappes, which is bordered by a coastward belt of folded crustal metamorphic and plutonic rocks. The first two structural zones are exposed in the Ouachita system in the Ouachita Mountains of Arkansas and Oklahoma (Goldstein, 1961), and in the Marathon Basin of western Texas (Flawn, 1961b); their presence has been thoroughly confirmed by deep drilling in the intervening region (Flawn, 1961c). The existence of a deeply buried belt of crustal folds is inferred for the Ouachita system (Flawn, et al, 1961), but has not been confirmed.

The Ouachita Structural Belt extends over a distance of about 2500 km, from eastern Mississippi west and southwest through the Ouachita Mountains, central and western Texas,

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and for an undetermined distance south into the Mexican Plateau. Stratigraphic evidence (summarized by King, 1961b) indicates that the Ouachita orogeny progressed in an east to west trend, occurring primarily in mid-Pennsylvanian time in the Ouachita Mountains region, but delayed until late Pennsylvanian and early Permian times in western Texas. In central Texas the margin of the Texas Craton, and particularly the Llano and Devils River Uplifts, served as buttresses against the Ouachita orogeny; this resulted in foreshortening of the frontal folded sedimentary zone and extensive overthrusting by the central nappe region, creating a steep mountain range during Permian time (Flawn, 1961e).

The Ouachita range in Texas was reduced by erosion in Permian, Triassic and Jurassic times to a subdued landscape termed the Wichita Paleoplain (Hill, 1901) or Comanche Shelf (Rose, 1972). This surface dips to the southeast at about 10 m per km, with irregular surface features of up to 100 m in relief (Flawn, 1961a), in addition to a larger regional rise associated with the Llano Uplift. Other major topographic features include a broad shelf, the Central Texas Platform (Rose, 1972) extending from north Texas to the region of the Llano Uplift, there bifurcating into a southwest-trending arch termed the Medina axis (Rose, 1972), and a southeastern promontory, the San Marcos Arch or Platform (Adkins, 1933; Rose, 1972). Combined, these slightly elevated features separate a pair of shallow basins. To the northeast of the Central Texas Platform and the Llano Uplift lies the

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broad North Texas-Tyler Basin (Fisher and Rodda, 1967); to the southwest lies a somewhat deeper depression termed the Maverick Basin (Winter, 1961; Smith, 1974).

The characteristics of this rise, platform and basin topography of the Comanche Shelf exerted significant influence on depositional events during the long Cretaceous inundation which gave rise to the rocks of the present Edwards Plateau. Deposition of the sediments comprising the Trinity Division of the early Cretaceous was affected by this landscape in two general respects, as outlined by Stricklin, Smith and Lozo (1971). The sloping edges of this surface resulted in the deposition of wedges of sediment thinning across the axis of the Central Texas and San Marcos Platforms and radially away from the Llano and Devils River Uplifts; further, the partial separation of the North Texas-Tyler and Maverick Basins effected by the Central Texas Platform contributed to the development of different depositional environments in these depressions throughout most of the Lower Cretaceous.

Depositional history

Starting in earliest Cretaceous times the region of the present Edwards Plateau was gradually covered by the epeiric sea which ultimately divided the North American continent on a north-south axis in the Late Cretaceous. A number of cycles of advance and regression of the sea characterized the Lower Cretaceous sequence in central Texas, resulting in a diversity of depositional environments and a corresponding

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diversity of rock types. Most of these environments were of broad areal extent, and the units produced can now be traced over long distances across the Central Texas and San Marcos Platforms. The sequence and terminology of units of the Lower Cretaceous rocks in the Edwards Plateau region are summarized in Table 2.

Lower Cretaceous strata in Texas are grouped into three Divisions (Trinity, Fredericksburg and Washita); the earliest (Trinity) sequence is partitioned into three units (lower, middle and upper). In a comprehensive review of Trinity stratigraphy and depositional environments, Stricklin, Smith and Lozo (1971) elaborate the conclusion that these units represent a trio of marine incursions and regressions. Each begins with terrigenous deposits of deltaic and beach materials and grades upward into shallow marine carbonates truncated by slight erosion marking the onset of the next incursive event. Owing to the progressive nature of transgression on the sloping surfaces of the basins and platforms lateral facies changes are the rule in Trinity sedimentary sequences; thus inland terrigenous deposits are the temporal equivalents of carbonate beds laid down offshore. In local outcrops the sand and shale sequences of the lower members of each couplet of the Trinity Division grade evenly into the upper limestone units by progressive reduction in the clastic contents of successively younger beds.

The lower Trinity cycle is composed of the Hosston Sand and Sligo Limestone; the shoreward facies of the latter is

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termed the Sycamore Sand. Both sand formations cover the Paleozoic rocks of the Comanche Shelf surface, and grade upwards or downdip into the Sligo Limestone of the first marine inundation. This couplet is of little significance in the present topography and hydrology of the Edwards Plateau apart from its role in reducing the topographic heterogeneity of the Paleozoic surface. The formations are restricted to the coastal margins of the present plateau and are deeply buried with the exception of a few exposures of the Sycamore Formation on the eastern limb of the plateau bordering the Llano Uplift (Amsbury, 1974, Plate 6). The Sligo Formation does not extend as far inland as does the Sycamore Sand and lies entirely in the subsurface.

The terrigenous phase of the middle Trinity cycle, the Hammett Shale, is similarly restricted in outcrop to the southeastern margins of the Llano region and is of little topographic or hydrologic significance. Its succeeding carbonate formation, the Cow Creek Limestone, is exposed in the drainages of the Colorado, Pedernales, Blanco and Guadalupe Rivers, and forms a locally significant aquifer in the last two regions of outcrop.

Lower and middle Trinity deposits are deeply buried in the Maverick Basin. Towards its margins and in the region of the Devils River Uplift these sequences thin markedly and merge as clastic deposits with the terrigenous materials of the third Trinity marine incursion into a thin zone generally referred to as the "basement sands" in the area to the south-

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west of the Central Texas Platform (Reeves and Small, 1973). No lower or middle Trinity deposits are exposed to the west of the axis of the San Marcos Platform.

The rocks of the third cycle of Trinity deposition, consisting of the Hensel Sand and Glen Rose Limestone formations, represent a major component of the present Edwards Plateau. During upper Trinity time and continuing through Fredericksburg and early Washita times the inland half of the present Gulf Coastal Plain and adjacent Edwards Plateau was a shallow lagoon developed behind the barrier reefs of the Stuart City Reef complex (Winter, 1961). Whether through uplift and subsidence or changing sea levels this 250 km wide lagoon underwent repeated fluctuations in depth during Lower Cretaceous times, ranging from tidal flats to protected bays 100 m or more in depth (Rose, 1972). The Hensel Sand of the upper Trinity cycle represents the last beach and/or deltaic environment in the Lower Cretaceous sequence. It is well developed only in the region of the North Texas-Tyler Basin and eastern San Marcos Platform, being absent or indistinguishable within the basement sands in the western part of the present Edwards Plateau.

The Hensel Formation is a thin (10-15 m) deposit in the outcrop, and is composed of gravel, sand, sandy dolomites and clay deposited in alluvial fans and beaches gradually covered by the invading sea. While easily removed by mechanical erosion, the high clastic content of the Hensel Sand makes it resistant to removal by solution; thus where the

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Hensel Formation lies close to the surface its contact with the overlying limestones of the Glen Rose Formation serves as an aquitard, promoting the development of long lateral cave passages. The resulting influence on the development of regional subterranean drainage systems is most pronounced in the middle section of the Guadalupe River drainage (see Chapter VI) but seems to be important in the adjoining Blanco River and Cibolo Creek drainages as well.

The upper surface of the Hensel Formation merges into the massive limestones of the lower Glen Rose Formation in passing vertically in the outcrop or offshore from the Central Texas Platform and Llano Uplift. As is the case with the deposits of the lower Trinity cycle the Hensel Sand and the lower portions of the Glen Rose Limestone merge in the region of the Llano Uplift into a formation termed the Gillespie Sand (Stricklin, Smith and Lozo, 1971).

The Glen Rose Limestone is separated into upper and lower members at a rather arbitrary level which is at variance with a clear environmental and structural boundary present within the formation. This boundary of convenience is a very thin but regionally extensive iron-stained bed of fossils of the clam Corbula texana, occurring within an extensive stratigraphic sequence of relatively thin tidal and evaporate deposits. A more meaningful divison might be made at the boundary between these beds and the massive underlying lagunal carbonates of the basal Glen Rose Formation. As presently recognized, two informal units are necessary with-

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in the lower Glen Rose Limestone to reflect the change from stable to unpredictable depositional environments (Stricklin, Smith and Lozo, 1971).

The basal Glen Rose Limestone is a massive, ledge-forming deposit composed of shell fragments in a limy mudstone or calcite matrix; it was apparently deposited in an extensive lagunal environment in which sedimentation rates roughly matched the rate of deepening of the sea (Stricklin, Smith and Lozo, 1971). This interpretation is supported by the existence of numerous patchy reef deposits (consisting of pelecypod shells and corals) at various levels near the base of the Glen Rose Formation along the southeastern flank of the Edwards Plateau (Perkins, 1969). These reef deposits are locally important in the formation of caves, as detailed in a subsequent section. In its area of outcrop along the Blanco, Guadalupe and Medina Rivers and Cibolo Creek the dense basal region of the Glen Rose Formation is marked by very extensive development of solutional features, with well developed subterranean drainage systems whose base level lies at or near the Glen Rose-Hensel Sand boundary.

The upper informal unit of the lower Glen Rose Limestone represents a change from stable shallow lagunal environments to a variety of tidal and supratidal situations; the resulting thin strata completing the lower member of the Glen Rose Formation are marked by extensive dolomitic beds and sandy limestones displaying algal mats, ripple marks, dessication features and dinosaur tracks. The upper member

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of the Glen Rose Limestone represents a continuation of shallow tidal and subaerial deposition. Its stratigraphic sequence contains eight traceable units of varying thickness and hardness in the eastern region of the Edwards Plateau; the sequence thins and cannot be traced across the axis of the Central Texas Platform, though beds of similar lithologies are widespread to the west (Stricklin, Smith and Lozo, 1971). Evaporite sequences of gypsum occur at the base and near the middle of the upper Glen Rose Formation; most of this material has now been leached away resulting in the collapse of overlying beds and creating locally important small aquifers. Otherwise, the high particle content and the thinness of the beds of the top of the lower Glen Rose together with those of the entirety of the upper Glen Rose retard the formation of interconnected solutional openings. For this reason little development of subterranean drainages is to be noted throughout the extensive region to the northeast of the San Marcos Platform where the land surface consists of upper Glen Rose Formation rocks. The topography of this region reflects the layered nature and varied composition of the strata, most hills presenting a "stairstep" outline, and most streams coursing along bedding planes with occasional low waterfalls or riffles where bedding planes are breached. Most of the (uncommon) springs of this region issue from the base of a breached stratum, and may simply represent underflow derived from joints in the channel bed upstream as opposed to the discharge of a significant aquifer.

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To the west of the San Marcos Platform the Glen Rose Formation preserves a basically similar sequence of lithologies, consisting of a thick, dense carbonate base overlain by thin beds of shale, shaly limestone and dolomite with local development of evaporite facies (Welder and Reeves, 1962). The lower member of the Glen Rose Limestone is not exposed west of central Bandera County, but it presumably plays an important role in the conduction of groundwater southeastward towards the extensive aquifer of the Balcones Fault Zone (Maclay, 1974). The upper member of the Glen Rose Formation forms the lower slopes and broad valley floors of the major drainages on the western limb of the Edwards Plateau, and its upper surface serves as a major regional aquitard where deposits of the overlying Edwards Group limestones remain extensive. The area of outcrop of the Glen Rose Formation is indicated in Figure 5.

Glen Rose deposits are overlain by a rather complex and regionally variable sequence of lower Fredericksburg Division formations, mediated by the influence of the Central Texas and San Marcos platofrms, the Medina Axis and the arcuate Devils River Trend bordering the Maverick Basin, in addition to the effects of the North Texas-Tyler and Maverick basins. Stratigraphy and the sequence of depositional environments in the region of the Edwards Plateau through Fredericksburg time have been ably synthesized by Fisher and Rodda (1967) and Rose (1972); much of the following discussion represents a distillation of this work and subsequent summarizations

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Figure 5. Outcrop regions of the lower unit of the Glen Rose limestones on the southern Edwards Plateau; the distribution of the upper Glen Rose outcrop inland from the fault zone may be visualized by comparison of Figures 5 and 6 (modified from Stricklin, Smith and Lozo, 1971).

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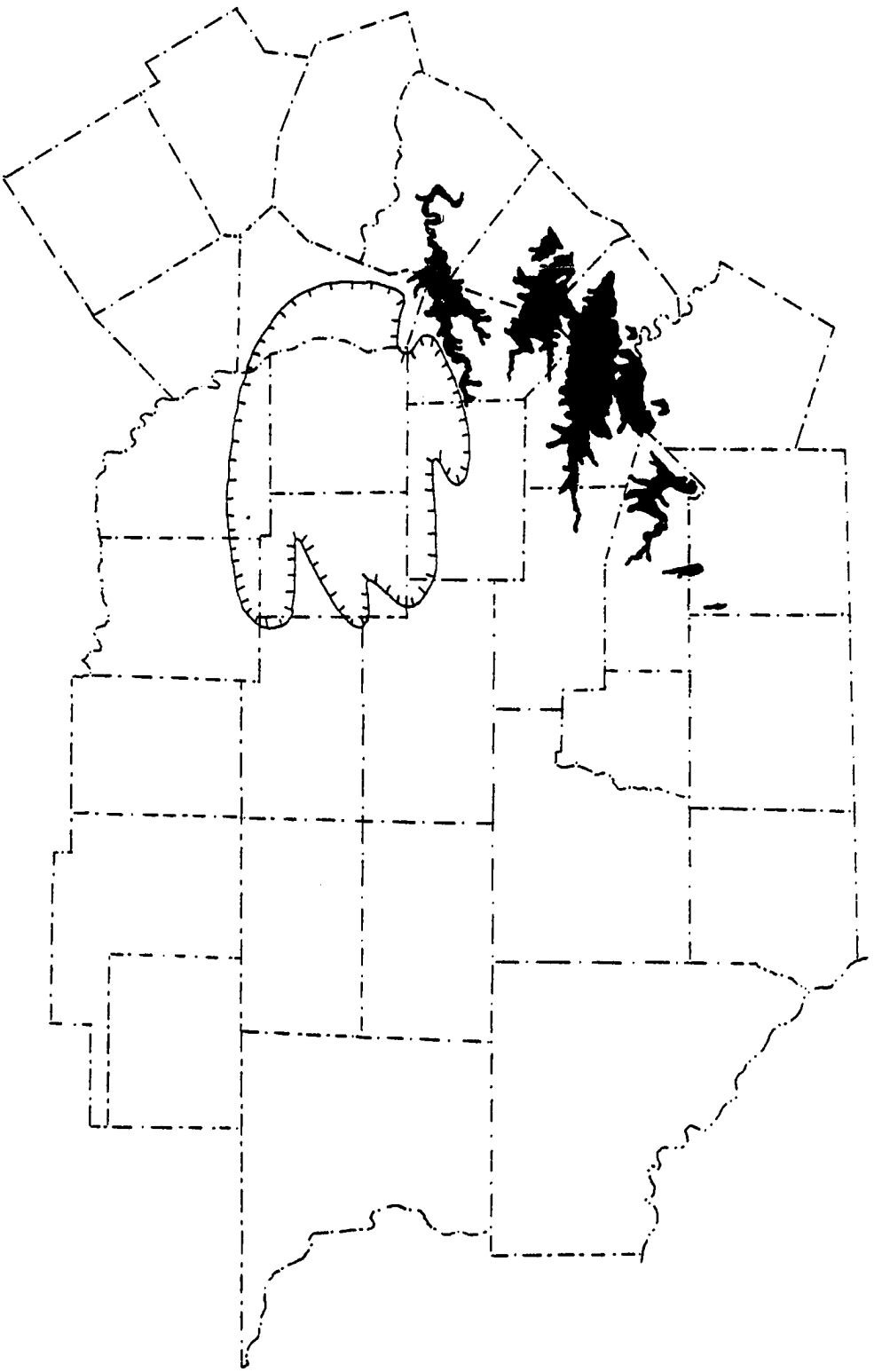

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(Rose, 1974; Smith, 1974). Rose (1972, p. 48) argues that the terms Fredericksburg Divison and Washita Divison are not applicable to the stratigraphic sequence above the Glen Rose Formation on the present Edwards Plateau owing to the absence of the implied discrete boundary between major cycles of sedimentation. In place of these divisions Rose redefines the major stratigraphic units of the plateau, the Walnut, Comanche Peak, Edwards, Kiamichi and Georgetown Formations of previous authors as the Edwards Group limestones. The Edwards Group consists of two formations, Fort Terrett and Segovia, with a complex series of lateral relations to several of the above-named and additional formations. The Fort Terrett and Segovia Formations are restricted to the Central Texas Platform, grading laterally into the Fredericksburg and Washita division formations of the North Texas-Tyler and Maverick basins. To the northeast of the San Marcos Platform the Glen Rose is conformably overlain by the Walnut and Comanche Peak Formations, both of which grade laterally into the Basal Nodular Member of the Fort Terrett Formation in the region southeast of the Llano Uplift. The Walnut Formation consists of fine clastics, grading into nodular silty marl in the Comanche Peak Formation. To the southwest of the San Marcos Platform Trinity deposits in the Maverick Basin are conformably overlain by the muddy limestones of the West Nueces Formation, which grade upward into the thinly bedded carbonaceous and muddy limestones and evaporite beds of the McKnight Formation (Lozo and Smith, 1964). The basal

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West Nueces Formation contains nodular and burrowed units comparable to those of the lower Fort Terrett Formation on the Central Texas Platform, but there the similarities end (Smith, 1974). Upper West Nueces and McKnight deposits reflect a restricted lagunal environment developed between the Stuart City Reef and the Devils River trend, a broad shallow bank of rudist reefs bordering the Central Texas Platform. Around the northern rim of the Maverick Basin the West Nueces and McKnight Formations grade laterally into the coarse, sorted bioclastic limestones of the slopes of the Devils River trend which comprise the Devils River Formation. Along their northern edge the deposits of the Devils River Formation grade rather abruptly into the Edwards Group Formations of the surface of the Central Texas Platform.

On the flanks and surface of the Central Texas Platform the Glen Rose Formation is slightly eroded and reworked, overlain by the 8-13 m thick marly zone of the basal Edwards Group. This zone is termed the Basal Nodular Member of the Fort Terrett Formation (Rose, 1972); as previously noted it represents the lateral equivalent of the Walnut and Comanche Peak Formations of the North Texas-Tyler Basin and the basal zone of the West Nueces Formation of the Maverick Basin. Overlying the Basal Nodular Member are the hard, porous limestones designated by Rose (1972) as the Burrowed Member of the Fort Terrett Formation; this zone constitutes the major aquifer of the central and western Edwards Plateau. The hydrologic significance of this 22-29 m thick series of beds

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owes to solutional removal of burrow fillings, thereby "producing superb honeycomb porosity" (Rose, 1972, p. 34), and to the widespread occurrence of dolomitic limestones and dolomite in overlying beds (Fisher and Rodda, 1967; 1969). Dolomitization is a diagenetic process which initially reduces the ability of carbonates to transmit water, because the relatively insoluble dolomite fills interstices within calcium carbonate rocks. The calcium carbonates are removed by solution leaving a latticework of dolomite (Ca, $MgCO_3$) which forms better reservoirs than do the calcitic limestones, for while pore size is reduced the pores are more continuous (Rose, 1967). Large solution channels are unlikely to form in dolomite but high permeability of leached dolomitic deposits forms an excellent diffuse aquifer.

The Fort Terrett Formation is completed by a pair of stratigraphic units, the Dolomitic Member (13-29 m) and Kirschberg Evaporite Member (13-26 m) (Rose, 1972), representative of increasingly shallow depositional environments on the Central Texas Platform (Fisher and Rodda, 1967; 1969; Rose, 1972). The superposition of the Dolomitic Member on the Burrowed Member results in a nearly ideal aquifer system, with the highly permeable upper unit serving as a reservoir which drains through the highly porous Burrowed Member; the relatively insoluble Basal Nodular Member forms a regional aquitard in the system, promoting lateral drainage through the Burrowed Member. For these reasons, essentially all of the reliable spring flow on the western limb of the Edwards

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Plateau inland from the Balcones Fault Zone and east of the Devils River canyon arises from the base of the Burrowed Member. The springs flow across the eroded outcrop slope of the Basal Nodular Member before sinking into the coarse alluvial deposits blanketing the top of the Glen Rose limestones.

The deposits of the Fort Terrett Formation are overlain by a heterogeneous assemblage of shallow marine sediments termed the Segovia Formation (Rose, 1972). The units of this formation tend to reflect progressive shallowing and restriction of circulation on the Central Texas Platform, proceeding from the open shallow marine environment which followed the tidal flats of upper Fort Terrett age upwards through a shallow tidal stage which was again submerged towards the close of the Segovia sequence (Rose, 1972, Fig. 35). In the Maverick Basin southwest of the Devils River trend the deposits of the Segovia interval are represented by pelagic limy mudstones grading into lagunal bioclastic limestones which together comprise the Salmon Peak Formation (Smith, 1974).

The Segovia Formation in the northwestern quadrant of the Edwards Plateau shares sufficient lithic similarity with the underlying Fort Terrett Formation that the topographic characteristics of the two formations constituting the Edwards Group can be considered together. Limestones of the Edwards Group form the surface of the entire western sector of the Edwards Plateau, and persist on the crests of the

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long divides radiating away to the east and south, in addition to a complex arc of outcrops throughout the eastern half of the Balcones Fault Zone. The distribution of outcrops of Edwards Group, Devils River Formation and Maverick Basin equivalent limestone is shown in Figure 6.

The constituents of the Edwards Group represent a sedimentary wedge which thickens to the south corresponding to the regional slope of the depositional surface. The Edwards Group thickens from about 130 to over 210 m in passing from the northwestern part of the present Edwards Plateau southward to the boundary of the Devils River Formation (Rose, 1972). As Rose notes, "largely because of this wedge-form, and because the resistant Edwards is the plateau-former, the top of the Edwards Plateau rises gently to the south before declining by erosion into the watersheds of the Frio, Sabinal, and Nueces Rivers" (1972, p. 7).

Wherever the lower portion of the Fort Terrett Formation is exposed reliable sources of surface water are to be expected. Surface drainage is virtually nonexistent on landscapes underlain by Edwards Group limestones owing to the presence of the several evaporite and dolomitic beds, and to the porosity of the lower Fort Terrett Formation. Solutional removal of the anhydrite and gypsum constituents of the evaporite members leads to the formation of collapse structures such as dolines in large numbers on the broad divides of the undissected plateau surface. The collapse process fractures solution-resistant beds of dolomite and shale,

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Figure 6. Areal extent of the Edwards Group and equivalent limestones on the Edwards Plateau. The overlying Del Rio and Buda Formation deposits in the Balcones Fault Zone are not indicated. This figure is based on Plate 1 of Rodda, et al (1966).

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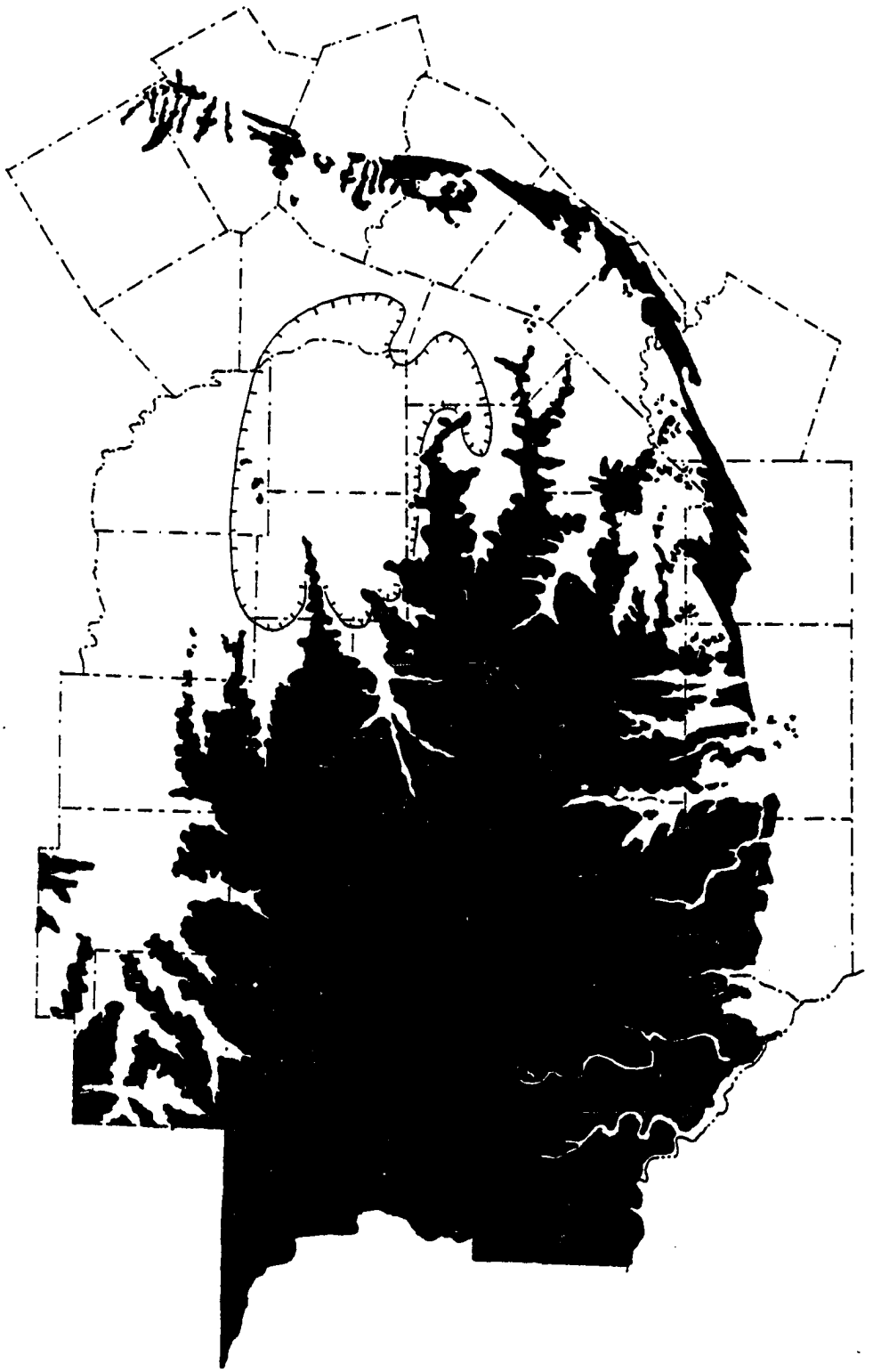

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permitting relatively rapid drainage of surface water collected in the dolines and leading to concentrated solutional removal of calcium carbonate from both dolomites and limestones, in the latter case eventually producing sinkholes. The high porosity of the Burrowed Member and the high permeability of the overlying Dolomitic Member of the Fort Terrett Formation allow relatively rapid transmission of groundwater along the regional dip of the upper Trinity surface to the points where this plane is transected by stream canyons.

The remaining Cretaceous deposits above the limestones of the Edwards Group contribute little to the structure of the present Edwards Plateau, with the possible exception of the middle Washita unit of the western plateau widely recognized as the Georgetown Formation (Welder and Reeves, 1962; Reeves and Small, 1973). On the eastern edge of the San Marcos Platform a unit of the same name is recognized, which together with the underlying Kiamichi Formation can be shown to grade laterally into the upper and lower beds, respectively, of the Segovia Formation (Rose, 1972). The correspondence of Kiamichi and Georgetown deposits with the Segovia Formation is not clear on the western plateau, largely as a result of reduced field investigation rather than owing to any intrinsic difficulty.

Part of this problem is simply nomenclatoral; the formations termed Kiamichi and Georgetown by Welder and Reeves (1962) in Uvalde County are now regarded as the McKnight and Salmon Peak Formations of the Maverick Basin (Lozo and Smith,

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1964; Smith, 1974), and the Devils River Formation extending along the western Balcones Fault Zone. As such they are the contemporaneous lateral equivalents of the Edwards Group limestones of the Central Texas Platform. At the level of the Devils River trend in Val Verde County Reeves and Small (1973) distinguish a "Georgetown Formation" overlying "Edwards Formation" rocks. By its position the latter appears to be the strict equivalent of the Fort Terrett Formation of Rose (1972), but it remains unclear whether or not the "Kiamichi Formation" and "Georgetown Formation" deposits are comparable to those of the upper Edwards Group. McKnight deposits pinch out in southern Val Verde County as expected of Maverick Basin sediments (Lozo and Smith, 1964); Reeves and Small, 1973; Smith, 1974), but "Georgetown" rocks extend across the western plateau as a massive (130-160 m thick) formation of major outcrop significance. The lateral equivalent of the Georgetown Formation of the North Texas-Tyler Basin reduces to a thin zone near the top of the Segovia Formation (Rose, 1972), requiring some explanation of the observed excess thickness of the "Georgetown" to the west of the Central Texas Platform. This explanation may lie in the observation that the boundary between the Segovia Formation and the overlying Del Rio Formation represents a major disconformity (Lozo and Smith, 1964; Rose, 1972). Rose (1972) interprets the regional variability in the distance between a marker bed in the upper Segovia Formation and the upper surface of Segovia deposits to reflect a period of sub-

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stantial erosion of the Segovia surface prior to Del Rio deposition. The inferred exposure of the Central Texas Platform during late Segovia/Georgetown time may have resulted in the removal of some "Georgetown" sediments as well as nondeposition of the upper "Georgetown" sequence on the platform. Deposition of these sediments continued apace west of the Central Texas Platform, resulting in the observed greater thickness of the "Georgetown" in this region. If this interpretation is correct the inland portion of the Georgetown Formation of Reeves and Small (1973) is a composite only partially equivalent to the Segovia Formation of Rose (1972). In that no division appears to exist within the western "Georgetown" deposits the whole formation can probably be included in the Edwards Group limestones. In the North Texas-Tyler basin the Georgetown Formation would remain excluded from the Edwards Group. The western "Georgetown Formation" north of the Devils River trend should probably be termed the Segovia Formation throughout the western Edwards Plateau, as inferred from Lozo and Smith (1964), Rose (1974) and Smith (1974).

The Segovia Formation on the western Edwards Plateau is more lithically uniform than the eastern Segovia, consisting of medium to massively bedded dense limestones with thin shaly intervals (Reeves and Small, 1973). Evaporite deposits appear to be lacking; thus the numerous collapse features seen in exposures of Segovia rocks inland from the Devils River trend and in the Devils River and Salmon Peak Forma-

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tions as well are the result of dissolution of carbonates alone. Subterranean drainage is the rule on these exposures, with only the deeply incised larger rivers (Devils and Pecos Rivers and the Rio Grande) maintaining surface flow, augmented by a few large springs (Brune, 1975). Small headwater springs are absent in the Devils River basin.

The upper surface of the Edwards Group limestones is a disconformity throughout the Edwards Plateau save in the Balcones Fault Zone (Rose, 1972; Reeves and Small, 1973), and is overlain throughout by the rather uniform clays and shales of the Del Rio Clay. This formation of terrigenous sediments represents an open marine environment marking the start of the definitive submergence of the entire Comanche Shelf in late Washita time. The Del Rio Formation grades evenly upward into the open shelf deposits of muddy limestones which comprise the Buda Formation. Available evidence suggests that the Buda Limestone evenly blanketed the entire Edwards Plateau region by the close of Washita time (Rose, 1972). Neither the Del Rio nor Buda Formations remain to any topographically significant extent on the present Edwards Plateau, having been stripped away following the uplift. No post-Washita deposits persist.

In summary, the Cretaceous sediments which comprise the Edwards Plateau reflect a number of cycles of marine incursion and regression across a broad continental shelf. The lithologic diversity resulting from this pattern was enhanced by the existence of persistent low topographic irregularities

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and the development of barrier and marginal reefs, all of which combined to exert significant local influence on depositional environments. The major building blocks of the present Edwards Plateau are the massive limy mudstones of the lower Glen Rose, Fort Terrett, Devils River and Salmon Peak Formations derived from shallow shelf and quiet lagunal environments, and the thin, variable beds of the upper Glen Rose and Segovia Formations which represent periods of tidal flat and restricted shallow lagunal environments. The beds of the former series are those of particular relevance in the development of karst features on the present plateau.

Tectonic History

The existence of the Edwards Plateau as a physiographic unit is a function of differential movements of very large regions of crust on either side of the long arcuate trend of the Balcones Fault Zone. Beyond the narrow confines of this intensely faulted band the strata of the Edwards Plateau and the Gulf Coastal Plain have remained largely undisturbed by tectonic events. Geologists have long noted the close correspondence of the trend of the Balcones Fault Zone with the underlying Ouachita Structural Belt. A good summarization of this relationship is provided by King, in observing that

> "...the inner edge of the area of subsidence, from Texas eastward to Mississippi, corresponds remarkably to the marginal part of the Ouachita system. Zones of normal faulting along the edge of the area of subsidence, such as the Balcones fault zone of Texas and others farther east, and zones of igneous activity of Cretaceous and early Tertiary age, closely follow the Ouachita trend. This

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> relation may be coincidental, but at the very least, the structures associated with the subsidence of the Gulf of Mexico utilized lines of weakness already created by the Ouachita system. Most likely, the Ouachita system and the Gulf of Mexico are manifestations of a single continuing process, the structural features of the latter having been inherited from those of the former" (1961b, p. 190).

This much is clear, and generally agreed. Much less agreement exists concerning the mechanisms and timing of the origin of the Edwards Plateau; the latter uncertainty is of particular importance here, as its resolution has important biogeographic consequences. Biologists in particular have seized on scraps of geologic information without considering the validity of their interpretations therefrom, and have in general been led to regard the origin of the Edwards Plateau as a relatively recent event, generally of latest Pliocene or early Pleistocene age (Mitchell and Reddell, 1971; Mitchell and Smith, 1972 represent examples of this tendency).

The mechanisms by which the Edwards Plateau was produced are closely related, at least in part, to regional tectonic events associated with the formation of the Gulf of Mexico. The subsidence of the Gulf is generally correlated with the formation of an extensive series of *en echelon* fault zones, of which the Balcones Fault Zone is the westernmost expression (Murray, 1961). Other fault systems tied into the regional pattern of subsidence include: the Luling Fault Zone, developed parallel to the Balcones Fault Zone along the in-

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land margin of the Stuart City Reef; the Mexia and Talco fault zones trending northeast and east through northeastern Texas; the South Arkansas Fault Zone extending across Arkansas to the south of the Ouachita Mountains; and the Pickens and Gilbertown fault zones trending southeast from west-central Mississippi into extreme northwestern Florida (Murray, 1961; Walthall and Walper, 1967a). All of these fault systems occur a few kilometers coastward from the crest of the Ouachita Structural Belt, and extend the scope of the general relationship between the Ouachita trend and the location of the Balcones Fault Zone noted above.

Two general models have been proposed for the origin of the peripheral Gulf fault systems; one depends on classical geomorphic processes, while the other is anticipatory of more general models of continental drift. Bornhauser (1958) advanced the view that the peripheral Gulf fault zones were produced through tensional stresses arising from plastic downslope movements of sedimentary beds into the developing geosyncline of the Gulf basin. This model also explains the formation of folded beds, and incorporates the observed igneous activity of the Gulf margins as plutonic intrusions into the faulted beds. Such intrusions were held to produce both local and regional uplifts, and one of the latter was genetically associated with the formation of a small rift valley in the South Arkansas system. A major difficulty with the plastic flow model is that the faults produced should all dip away from the Gulf basin. Various local differences from

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the regional dip are advanced in explanation, but these seem to violate the premise that plastic flow is feasible only under conditions of high mass loading, which seems unlikely in restricted slope reversals.

Walthall and Walper (1967a) reformed this difficulty into the primary evidence for a new model of Gulf Coast tectonics based on rift faulting, still associated with the development of the Gulf geosyncline. They note that the northern margin of the Gulf Coastal Plain is lined with a nearly continuous belt of opposing, or antithetic, faults defining a peripheral Gulf rift zone comparable to those of Europe and eastern Africa. In this interpretation the down-to-the-coast faults of the Balcones Fault Zone are paired with the roughly parallel up-to-the-coast faults of the Luling Fault Zone to define an included rift valley in the subsurface; antithetic components and small rift valleys are also present within the Mexia-Talco, South Arkansas, Pickens and Gilberstown Fault systems. Tensional faulting and igneous intrusions are predicted by this model as well as by the plastic flow model, but the two seem to differ in one important respect (not noted by Bornhauser or Walthall and Walper): intrusive activity should be more frequent within the grabens of the rifts than on either side of the antithetic fault system in the rifting model, whereas no such localization is predicted by the plastic flow model. As is clear from Plate 1 of Lonsdale (1927), igneous intrusions are far more frequent and of larger scale coastward of the faults

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delimiting the Edwards Plateau than they are on the plateau proper, even though the plateau represents a much lower geologic horizon than does the adjacent fault zone and Gulf Coastal Plain.

The proposition of a rift model for the origin of the well-studied peripheral Gulf fault systems drew immediate comments by Bornhauser (1967) and Meyerhoff (1967), with replies by Walthall and Walper (1967b;c). The former questioned the sufficiency of the evidence for recognizing rift valleys; however, Walthall and Walper cite eight satisfied criteria against the one missing (which actually occurs in the South Arkansas system). Meyerhoff (1967) pointed out that the secondary incision observed in the marginal drainages of the Edwards Plateau constitutes evidence that the plateau has been elevated, in contrast to the rift (and plastic flow) model(s), which predict that the Gulf Coastal Plain has subsided. Walthall and Walper (1967c) suggest that this relationship may be independent of the mode of origin of the faults themselves, involving instead the greater structural stability of the San Marcos Platform underlying the region of incised streams in question. Further, they note that it is only in this region that the Balcones Fault Zone maintains a significant escarpment, associated with the greatest vertical displacement of any faults within the Balcones system. An alternative explanation of second-cycle incision based on lithologic differences between fault zone and plateau terranes will be detailed in a subsequent section.

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The rift model thus appears to assimilate the major difficulty of the plastic flow model, and in addition successfully predicts the observed localization of igneous activity. Subsidence of the Gulf Coastal Plain, possibly in conjunction with elastic rebound of the strata of the plateau proper following faulting, appears to be the mechanism of origin of the Edwards Plateau.

The timing of the definition of the Edwards Plateau as a positive structural feature has been difficult to assess, as no precise temporal correlation necessarily exists between the existence of significant relative elevation and most of the available evidence derived from faulting, igneous intrusion and erosional processes prior to Quaternary times. In a regional sense the weight of evidence supports two conclusions: that activity of the peripheral Gulf rifts has been of an intermittent nature (Lonsdale, 1927; Bornhauser, 1958; Walthall and Walper, 1967; Young, 1972); and that the process probably began in the early Upper Cretaceous and continued through Tertiary and into Quaternary time (Lonsdale, 1927; Young, 1972). Evidence that movement along the Balcones Fault Zone continues today was noted by George (1952) in demonstrating that low rapids are present in the bed of the Guadalupe River where it crosses the Hueco Springs Fault in Comal County. Despite this evidence, there are essentially no records of earthquake activity in the region in historic times.

Igneous intrusive activity is widely apparent along the

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trend of the Balcones Fault Zone, particularly in Uvalde, Kinney and Travis Counties (in decreasing order). These volcanic rocks consist of small basaltic plugs, dikes, and sills penetrating Lower Cretatceous sediments, and layers of serpentine and bentonite interbedded with limestones of early Upper Cretaceous age. Serpentine is a weathering product of basalt and thus its interbeds can be considered to be of local origin, whereas bentonite is derived from windborne volcanic ash and is not reliable as an indicator of local volcanic activity.

In an extensive review of the occurrence and petrology of the igneous deposits of the Balcones Fault Zone Lonsdale (1927) demonstrates two periods of significant volcanic activity:

> "The igneous activity recorded by the massive rocks [plugs, dikes and sills] and here assigned a Tertiary age, is probably early Tertiary" (p. 46).
>
> "It is certain also that igneous rocks were formed in the area as early as Eagle Ford, Austin, and Taylor times [middle Upper Cretaceous]. No remnants of solid rock bodies of these ages are known, but the interstratified bodies of serpentine rock found in the Eagle Ford in Uvalde County and in the Austin and Taylor formations, near Austin and elsewhere, are ample evidence for this conclusion" (1927, p. 45).

Lonsdale suggested that volcanic activity was continuous at a low level in the intervening period; subsequently Young (1972) was able to elaborate that:

> "It was during Austin time that volcanism forecasting the future site of the Balcones fault zone seems to have been most dominant. Volcanism actually began in the Del Rio

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> (Cenomanian) and continued into Navarro (Maestrichian) [thus, the entire Upper Cretaceous] " (1972, p. 44).

These interpretations were mostly derived from stratigraphic evidence such as the stratigraphic positions of sills and serpentine beds, and the local displacement and contact metamorphism of adjoining strata by plugs. Deposits of detrital serpentine and other volcanic debris generally provide more precise temporal data than do primary intrusive bodies in that sills may form at any level in the geologic column, and because erosionally exposed plugs are difficult to date by stratigraphic criteria in the absence of local interbeds of igneous debris. In view of the uncertainty inherent in these methods it is fortunate that Baldwin and Adams (1971) have determined the crystallization ages of the primary intrusive structures of the Balcones Fault Zone by potassium-argon dating methods. Samples of erosionally exposed igneous rocks from Kinney, Uvalde and Travis Counties range in age from 86 ($\pm$5) to 63 ($\pm$2) million years before present, with 13 of the 15 intrusions being 73 million years of age or older; two samples are dated at 63 million years and may represent a second period of intrusive activity (Baldwin and Adams, 1971, Table 1). The Travis County sample is dated at 79.5 million years, comparing closely with the average age of 78.5 million years of the older subset of Uvalde and Kinney County rocks. If the assumption is made that the intrusion of magma along the Balcones Fault Zone was correlated with the inception of major faulting activity, such activity was cen-

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tered in the early and middle Upper Cretaceous, during the deposition of late Washita, Woodbine, Eagle Ford and Austin Division rocks; limited activity seems to have occurred at the Cretaceous-Tertiary boundary as well. These times are concordant with those reached by Lonsdale (1927) and Young (1972), though Lonsdale assigned all of the primary intrusive rocks to the Cretaceous-Tertiary boundary and relied on serpentine deposits as evidence of Cretaceous volcanic activity.

It seems probable that a certain amount of movement occurred along the Balcones Fault Zone during the Late Cretaceous, but there is no evidence that it was of sufficent magnitude to raise the Edwards Plateau much above the level of the epeiric sea, except perhaps in the region of the Llano Uplift; in any case such stratigraphic evidence of this movement as may have existed has been long since removed by erosion. Young (1972) concludes that the Llano Uplift, submerged by late Fredericksburg time, was again near or above sea level by middle Washita (Del Rio and Buda) times, and was sufficiently elevated during Eagle Ford time to serve as a source area for the numerous fossil logs found in Eagle Ford deposits. Rose (1972) cites the presence of logs in the upper Edwards as evidence that the Llano region was elevated somewhat earlier. The uplift seems to have been submerged during the remainder of the Upper Cretaceous (Austin, Taylor and Navarro times), as was the entirety of the present Edwards Plateau. The degree of influence of movement

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in the Balcones Fault Zone on this pattern of elevation and subsidence of the Llano Uplift is conjectural.

With the retreat of the Cretaceous seaway which marks the earliest Tertiary, evidence of the erosion of elevated regions bordering the Gulf of Mexico can be sought in the sediments deposited on the Gulf Coastal Plain. The sequence of Upper Cretaceous deposits to be removed by erosion consists of rocks from which little concrete evidence of secondary deposition can be had from analysis of Gulf Coastal Plain deposits. The thick strata of this time interval (Navarro, Taylor, Austin, Eagle Ford, Woodbine and Washita Divisions) are all rather "clean" formations consisting of either fine clastics such as shales and clays (Navarro, Taylor, Eagle Ford) or nearly pure marine carbonates (Austin, Washita). Most erosion of carbonates is by solution, which deposits no recognizable sediment, and the presence of reworked clastics from erosion of the remaining deposits intermixed with sediments from other sources in the Gulf Coastal Plain is perhaps impossible to detect. Neither chert nor appreciable amounts of other macroscopic insoluble materials occur in any Upper Cretaceous deposits in the Edwards Plateau region apart from the fossil trees of the Eagle Ford Shale and upper Edwards Group limestones. Evidence of the erosion of these deposits might be sought in Paleogene sediments of the Gulf Coastal Plain, but in general the wrong facies are exposed on the outcrop; reworked fossils other than foraminiferans are unlikely to be found in these fine

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clastics. Even if possible, the prospects for close temporal resolution are slim, in that most Cretaceous foraminiferan taxa are of broad temporal range (Frizzell, 1954).

Evidence is developing that a major tectonic change occurred in central Texas towards the close of the Eocene and continued at least through Miocene times. During the early Eocene a major portion of the continental interior was drained through central Texas, as indicated by the formation of a major delta system along the coast. The Rockdale Delta System of the Lower Wilcox Group (Fisher and McGowen, 1967) was roughly twice the size of the contemporaneous system in the Mississippi region, and shows characteristics of deposition by a fluvial system with a distant source (possibly extending to the continental divide) (Fisher and Mcowen, 1967; Galloway, 1968; Fisher, 1969). In the later Eocene, delta systems of the Jackson-Yegua Group are reduced in size in comparison to those of the Lower Wilcox (Fisher, et al, 1970), and may indicate an eastward shift of the major continental drainage system. This shift, and the existence of small deltas along the south Texas coast which increased in size from Jackson through Yegua times (Fisher, et al, 1970, Fig. 15) are suggestive of uplift in the region of central Texas. The Jackson-Yegua deltas are characteristic of near-source fluvial systems, perhaps draining an elevated Edwards Plateau (Fisher, 1969).

Oligocene and Miocene delta systems in Texas continue this trend towards small, near-source deltaic deposits (Fish-

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er, 1969; Boyd and Dyer, 1964), as the major continental drainage shifted to the Mississippi basin. The earliest indisputable evidence of the existence of the Edwards Plateau is found in the Oakville Sandstone of early to middle Miocene age (Weeks, 1945b; Fisher, 1969). The Oakville is the earliest local Gulf Coast depositional system in which coarse clastics are exposed; probably on the basis of this evidence Young (1972) states that:

> "It was at this time that most, if not all, of the movement on the Balcones fault zone raised the Llano uplift-San Marcos Platform to such height that most of the Navarro, Taylor, and Austin rocks were stripped off and redeposited in the Gulf Coast geosyncline" (1972, p. 44).

However, the sediments which comprise the Oakville Formation clearly indicate that removal of the Upper Cretaceous deposits of the Edwards Plateau was well advanced by middle Miocene. The Oakville Formation consists of calcareous clays and cross-bedded sandstones containing reworked Cretaceous shell fragments, abundant limestone gravel, and most significantly, gravels of chert, quartzite and igneous rocks (Weeks, 1945b; Fisher, 1969). None of the Cretaceous formations younger than the Segovia contain appreciable amounts of chert (Geologic Atlas of Texas, 1974); thus the interclasts of the Oakville Formation must represent erosion of Edwards Group limestones, and the younger Cretaceous deposits must have been removed prior to mid-Miocene. The identities of the reworked Cretaceous fossils in the Oakville Sandstone are not reported by Weeks (1945b), but Bailey (1923) reports

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reworked Exogyra arietana in the upper Oakville; this pelecypod is most abundant in the lower Del Rio Formation on the present Plateau (Geologic Atlas of Texas, 1974). Maxwell (1970) has commented that "many of the Oakville beds contain reworked invertebrate fossils from the Cretaceous rocks... This indicates uplift along the Balcones fault zone...during the Oakville epoch" (p. 148)

The Fleming Formation of late Miocene age and the Pliocene Goliad Formation also contain large amounts of chert gravel, indicating continued active erosion of Fredericksburg rocks of an elevated Edwards Plateau (Weeks, 1945b).

All of these indications of the existence of an erosionally dissected plateau during middle and late Tertiary have been overlooked by biologists and biogeographers. For example, Barr (1960) suggested that even in the Balcones Fault Zone (where earliest erosional exposure and development of caves would be expected) the formation of caves was an early Pleistocene event. Mitchell and Reddell (1971) acknowledge that:

> "It is barely possible that some fault zone caves might have been available for colonization in the late Miocene, but is more likely that this was a Pliocene event. It is even possible that the fault zone caves were not opened until early Pleistocene. Subterranean systems in areas removed from the fault zone were probably not available for colonization until mid-Pleistocene" (1971, p. 357).

Holsinger (1967) accepts a similar time scale.

Most of this advocacy of a Quaternary origin of erosional dissection and formation of caves on the Edwards Pla-

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teau owes to acceptance of early geological discussions of the implications of a chert-bearing formation termed the Uvalde Gravel (see Hill and Vaughan, 1898; Vaughan, 1900; Hill, 1901; Sellards, Adkins and Plummer, 1933; Sayre, 1936; and Byrd, 1971). As summarized by Weeks (1945a, Fig. 1) and Byrd (1971), deposits of the Uvalde Gravel occur along the Rio Grande from the plateau southeast to Hidalgo County, in a broad irregular sheet reaching from the Balcones Fault Zone of Kinney, Uvalde and Medina Counties southeast to McMullen County, and in isolated southeast-trending patches along the Balcones Fault Zone from San Antonio to Austin. More recent work (Geological Atlas of Texas, 1974) suggests that the Willis Formation, a siliceous gravel deposit of broad areal extent on the Gulf Coastal Plain southeast of the eastern limb of the Edwards Plateau, may correlate with the Uvalde Gravel to the southwest. Byrd (1971) suggests that the Uvalde Gravel may be derived at least in part from the Ogallala Formation, a late Tertiary clastic deposit which blankets much of the southern Great Plains. The entire irregular band of the Uvalde, consisting of chert and limestone cobbles and gravel is variously attributed to the latest Pliocene or early Pleistocene (Aftonian and Peorian interglacials). Close to the Balcones Fault Zone it forms high stream terraces, which in the maturely eroded eastern plateau region are set well above present stream levels; this evidence is apparently taken to indicate Quaternary backcutting of drainages into the plateau margin, and a correspondingly recent

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origin of the plateau. This interpretation contains three errors: the implicit assumption, largely rejected by Byrd (1971) that the Uvalde Gravel is derived from the chert deposits of the upper Edwards Group; the failure to consider the source of the cherts of the Oakville and Fleming Formations clearly indicative of Miocene erosion of Edwards Group limestones; and the failure to incorporate the implications of the second-cycle rejuvenation evident in the drainages of the eastern plateau (Meyerhoff, 1967). This last error of interpretation results in the comparison of the terrace levels of the Uvalde Gravel with present stream levels, with misleading results. A reinterpretation of the significance of the Uvalde Gravel to conclusions about the degree of erosional dissection of the eastern Edwards Plateau at the Plio-Pleistocene boundary is developed in the section below.

Erosional History

From the evidence presented above it is clear that the Edwards Plateau has existed as an elevated structure since at least the middle Tertiary, and possibly for the duration of the Cenozoic. On the far western limb of the Plateau, Thomas (1972) has suggested regional uplift beginning in the Eocene to explain the present course and incised canyon of the lower Pecos River. The pre-Miocene record of the progress of erosional dissection of the plateau surface is probably lost, and the information available from Miocene deposits is of restricted utility. The only thing certain

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is that the Edwards Group limestones of the eastern limb of the plateau were exposed and undergoing erosion by mid-Miocene time. Mench (1978) has stated that the Balcones Aquifer originated in the Miocene, which presupposes the existence of an elevated plateau by that time. The record of Pliocene and Pleistocene events is somewhat better, but this information has apparently never been synthesized. In a very general way the physiography of the present Edwards Plateau may provide a reasonable model for the interpretation of past events. Owing largely to the nearly perpendicular orientation of the plateau to the coast of the Gulf of Mexico annual rainfall decreases in a regular fashion in passing westward, from about 80 cm in the region of Austin to less than 40 cm west of Del Rio. A primary correlate of this gradient is seen in the trend from mature to moderately youthful erosional stages displayed along this same east-west axis. The regional uniformity of Fredericksburg and Washita rocks across the plateau lends some confidence to the suggestion that the morphology of the western plateau drainages today may reflect the appearance of the eastern drainages at an earlier time. The earliest development of plateau drainages on upper Cretaceous deposits may have a modern counterpart in drainages on these rocks in north-central Texas, but this similarity is sufficiently conjectural that only the broadest generalizations seem tenable. In particular contrast the modern north Texas drainages lack the moderate to strong hydrologic gradient provided by the

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activity of the Balcones Fault Zone to the south during early Tertiary times.

Any discussion of the erosional history of the Edwards Plateau must remain speculative and to a large extent unverifiable. The treatment attempted in the next few pages is recognized to be so, but is at least constructed on general principles of hydrology and from a familiarity with the regional geology and topography. It is felt to be a useful exercise, because it succeeds in explaining several of the previously unresolved structural pecularities of the present Edwards Plateau. Much of the discussion rests on the validity of the assumption that the physiographic trends observable on the present plateau bear some relation to temporal trends in single drainages. Little reference is made to the effects of climatic variation, as the discussion is intended to provide only a model of the sequence of events without reference to the rates at which they proceeded or the precise time intervals in which they occurred.

Except for the Colorado River, the Pecos River and the Rio Grande the drainages of the Edwards Plateau give every indication of having developed in place subsequent to the origin of the plateau. As the plateau developed, the early drainages on the Upper Cretaceous surface probably adopted classic dendritic drainage patterns in their headwater areas, with wide shallow valleys extending headward from the plateau margins. The centripetal pattern of drainage axes and the scarcity of incidents of stream capture suggest that the

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present plateau drainages are contemporaneous, and may reasonably reflect the original distribution of streams. Recently Woodruff (1977) has pointed out an instance of stream capture on the eastern limb of the plateau which may have occurred during the Miocene; if valid, this observation substantiates the general time frame suggested herein. Erosional downcutting probably proceeded rapidly through the marls and shales of the entire Gulf Series (Navarro, Taylor, Austin, Eagle Ford and Woodbine Divisions), producing a landscape of broad shallow valleys and wide flat divides which remained relatively stable until the major drainages reached harder Comanche Series rocks in the early Miocene. As Young notes "...when erosion had cut down to the Buda, and the Edwards Limestone [=Segovia Formation] where the Buda is absent, erosion was slowed to a snail's pace" (1972, p. 46). This pronounced increase in erosional resistance and bed load must have resulted in markedly decreased stream gradients; this factor coupled with inherited drainage patterns probably led to the early formation of subterranean drainages, lacking until this stage owing to the incompetence of most Gulf Series Formations to form caves. In this interpretation the middle sections of the Miocene drainages were for a time perched above their normal gradient levels and losing water into the subsurface, contributing to the dissolution of the Edwards Group limestones inland from the Balcones Fault Zone. The entrenchment of the main valleys during this stage is probably represented by the appearance of

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coarse clastics in the Oakville Formation.

The drainages of the eastern plateau during the middle Miocene may have been physiographically similar to present river valleys of the western plateau such as the Devils, Dry Devils and West Nueces Rivers. These valleys are currently in youthful erosional stages, having deep, narrow canyons bordered by cliffs, and tributaries which are perched above grade for most of their lengths. Dolines and sinkholes are extensively developed both in tributary channels and on the broad divides; most of these solutional features are still very shallow. Springs are uncommon and restricted to the large river canyons (though this situation is chiefly the result of low rainfall -- in wetter areas springs would probably arise at several levels in the Segovia Formation). These three rivers presently have massive bed loads of chert and limestone cobbles, which the streams are incompetent to transport except during storms; most of the flow in normal periods is interstitial.

The extensive aquifer associated with the Balcones Fault Zone was probably established during the early stages of erosion of the Edwards Group landscape, as such development was necessary to balance the high recharge potential of the perched drainages of the plateau. The age of the aquifer has been recently stated to be Miocene (Abbott, 1974; 1975; Mench, 1978). Much more of this aquifer may have been under artesian conditions than is presently the case, from the postulation that the competent strata then lay at greater

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depths in relation to the elevation of the recharge surface.

The displaced position of Edwards Group limestones in the Balcones Fault Zone relative to these strata on the plateau proper seems to have been influential in the subsequent development of the marginal drainages. During the early ontogeny of these drainages this band of resistant rock was covered by softer Gulf Series deposits which presented no obstacle to the maintenance of efficient stream gradients across the Balcones Fault Zone. The displacement of Edwards Group limestones across the central third of the length of the Balcones Fault Zone is such that these strata were intersected by the major streams at about the time that their upper sections reached the top of the Glen Rose Formation deposits. Erosion proceeded rapidly in this zone of marls and thin-bedded shales and limestones while being somewhat restricted in the Balcones Fault Zone, ultimately resulting in the development of valleys in the plateau interior communicating with the Gulf Coastal Plain through narrow entrenched canyons.

Examples of this stage in the development of the plateau drainages are to be seen in the canyons of the Frio and Sabinal Rivers, and in a slightly more advanced condition in the valley of the Medina River. The former two drainages have narrow valleys developed on upper Glen Rose strata beginning just inland from the Balcones Fault Zone, with low-gradient tributaries extending to the Glen Rose-Edwards Group contact, then steepening abruptly, producing very

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highly dissected dendritic divides in the Edwards in which large scale development of solutional features is absent. Surface runoff probably represents a larger component of total recharge here than in the Nueces, Dry Devils and Devils River basins to the west. This point notwithstanding, the major source of recharge to the Frio, Sabinal and Medina Rivers remains that from groundwater collected on the undissected plateau surface to the north. As previously noted, the lower Fort Terrett Formation of the Edwards Group is a major aquifer, supplying permanent springs wherever it is intersected by tributary canyons. The major streams on the Glen Rose-surfaced valleys are not entrenched, and show low hydrologic gradients owing to the high bed load of lag gravel produced by erosion of the Edwards surface upstream. Owing to these conditions and the presence of the resistant beds in the fault zone downstream continued lateral development of the valleys is facilitated. The lateral growth of valleys based on upper Glen Rose deposits is mediated by undercutting of the overlying Edwards. Because the soft Glen Rose strata and the Basal Nodular Member of the Fort Terrett are mechanically eroded away at a higher rate than the harder overlying Edwards, the latter spalls off in large blocks. This process results in both the steepness of tributary canyons in the Edwards and the creation of a tremendous bed load of massive clastic cobbles, which greatly reduces the downcutting ability of the major drainage. Thus broad, nearly level valleys are produced inland from the fault zone.

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Under these conditions the streams may be expected to develop meanders, and such are apparent not only in the Frio, Sabinal and Medina valleys but in those of the eastern limb of the plateau as well.

Both of the apparent criteria for the development of broad internal valleys on the Edwards Plateau are of limited temporal extent. The rate of downcutting through the Edwards Group limestones of the fault zone might be considered an insignificant variable if the effect is viewed solely in terms of a damming function, but it is also necessary to incorporate the role of the fault zone rocks as the recharge surface for the fault zone aquifer. Under normal flow conditions the Frio, Sabinal and Medina Rivers drain heavily into the subsurface in the Balcones Fault Zone, greatly reducing the ability of these streams to erode their beds. Even so, this effect is thought to be secondary in importance to that of the lag load of these streams, and perhaps the saturation of the valley floor by discharge from the basal Fort Terrett Formation. As long as the lag load and the level of the water table in these valleys remain high very little vertical development of the drainages will take place below the headwater regions, though lateral extension and backcutting of the valleys should proceed unimpeded. The stable surface of the flood plain is ultimately disrupted by the very process it engenders, namely the lateral development of the valley floor at the expense of the Edwards Group limestones of the divides.

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At present the valleys of the Frio and Sabinal Rivers are well separated downstream as far as the inland margin of the fault zone by dissected uplands. It should be noted that these divides are composed of Devils River rather than Edwards Group limestones, but the lithologic and hydrologic relationships of the two to the underlying Glen Rose are essentially the same; numerous springs arise from the basal Devils River Formation and maintain saturation of the upper Glen Rose surface, and the Devils River contributes to bed loading in the same way as does the Edwards. The Sabinal valley is separated from the Medina valley to the east by the small drainages of Seco and Hondo Creeks, which have developed similar internal valleys but differ in having slightly entrenched channels near the fault zone. Such channel entrenchment is pronounced in the lower portion of the Medina valley on the plateau, indicating a reduced level with respect to the valley floor. In each of these cases, and especially in the Medina drainage, entrenchment begins at the level at which the Devils River or Edwards Group limestones of the divides begin to be reduced to narrow ridges and isolated caps. The suggested relationship is twofold: first, that the diminution of the Edwards divides results in a major reduction in bed load, increasing the competence of the drainage to entrench; and second, that the divide aquifers carry decreased amounts of groundwater, resulting in a decline in the water table in the upper Glen Rose strata of the valley and a corresponding entrenchment of the drainage.

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As the main drainage entrenches its tributaries remain perched above the water table, facilitating the development of subterranean drainages along the margins of the valley. A few small dolines are developed in the middle region of the Medina valley, but moderate development of sinkholes and subterranean drainages is limited to the lower valley region adjacent to the Balcones Fault Zone. This relationship cannot be considered to be solely the result of increasing entrenchment, as the shift from slight to moderate development of subterranean systems takes place near the transition from upper to lower Glen Rose deposits on the valley floor, and only the latter rocks are competent to form and maintain solutional channels. The rate of entrenchment seems to be independent of the lithology of the streambed, however, because the profile of the Medina River shows no perturbation at the contact between upper and lower Glen Rose deposits. This fact suggests that the elevation of the water table is more influential than streambed lithology in determining the location and degree of entrenchment. Extensive subterranean systems are primarily influenced by lithology, but develop most rapidly in areas of perched drainages; for both of these reasons the valleys of Hondo and Seco Creeks, and the valleys of the Sabinal and Frio Rivers inland from the Fault Zone show little development of subterranean drainages.

The middle drainages of the Edwards Plateau discussed above are more mature in their erosional characteristics than are the Sabinal and Frio drainages, and the latter are

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more mature than the drainages farther to the west. To the east and northeast of the Medina drainage the valleys of Cibolo Creek and the Guadalupe and Blanco Rivers display further maturation. As is apparent from Figure 6 the Edwards Group limestones are restricted to the upper half of the Guadalupe drainage, and approximately the upper third of the Blanco drainage; Cibolo Creek has only a small headwater divide of Edwards Group limestones remaining. These three drainages have similar rainfall regimes owing to their similar orientation along an east-west axis, and thus do not display the regular longitudinal progression in degree of erosional maturation characteristic of the drainages of the western plateau. Here basin size seems to be the important factor in determining erosional stage; the river with the largest basin (the Guadalupe) is the most mature, and the smallest (Cibolo Creek) is the least mature -- the Blanco River is intermediate in both respects. For these reasons these drainages are discussed in the sequence Cibolo Creek-Blanco River-Guadalupe River.

The valley of Cibolo Creek is largely developed on lower Glen Rose rocks, and the channel is only slightly entrenched -- less so than would be predicted from the foregoing discussion, as adjacent deposits of Edwards Group limestones are essentially lacking. Under these conditions the channel should be deeply entrenched, with extensive development of subterranean systems along the valley margins which communicate with the incised streambed. In fact, sub-

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terranean drainages are more extensively developed here than is the case anywhere else on the coastal segment of the Edwards Plateau, but the bed of Cibolo Creek remains perched high above the local water table throughout most of its length. This apparent contradiction to the general model (i.e., the lack of entrenchment) seems to have a simple causal basis which exempts it from a negating function: Cibolo Creek is the only plateau drainage which runs parallel (rather than perpendicular) to the Balcones Fault Zone, and the fault zone forms the southern boundary of the Cibolo valley for most of its length. The subterranean drainages of the Cibolo valley are directly linked with the aquifer of the Balcones Fault Zone rather than having any connection to the channel of the creek. These systems are so large, and so efficient in intercepting and removing surface flow that the creek itself very rarely flows. Two examples may serve to make this point. Following a storm on 29 August 1946, George (1952) observed an estimated discharge of 8500 l/sec in Cibolo Creek 18 km upstream from the gaging station at Bulverde, Comal County; the records of this station show that none of this flood water reached Bulverde (George, 1952, Table 18). On 5 October 1969 a violent thunderstorm at the headwaters of Cibolo Creek increased stream flow at Boerne, Kendall County from 145 to 21,600 l/sec; mean flow rates for the following 6 days were 2,830, 1,700, 1,218, 990, 880 and 765 l/sec. Discharge records were not kept at Bulverde, but the gaging station at Selma, Bexar County, 45 km southeast

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of Boerne at the edge of the Edwards Plateau, recorded no flow in Cibolo Creek during October 1969 (U.S. Geol. Survey, 1974). Calculation from the mean discharge rates listed above indicates that about 2.6×10^9 liters of surface runoff were captured by the subterranean systems along Cibolo Creek during this seven day period without exceeding their capacities. I have been unable to find any instance of recorded flow at the Selma gaging station resulting from rains restricted to the upper portion of the Cibolo Creek drainage.

Cibolo Creek thus presents a combination of a moderately youthful valley and a mature subterranean drainage system on the inland side of the Balcones Fault Zone. In view of the extensive development of subsurface systems in this region and their hydrologic association with the Balcones Aquifer rather than the lower Cibolo drainage I use the term Cibolo Sinkhole Plain in reference to the valley of Cibolo Creek between Boerne, Kendall County, and the inner margin of the Balcones Fault Zone.

The valleys of the Blanco and Guadalupe Rivers are representative of the most mature erosional stage on the present Edwards Plateau, in which the lateral development of interior valleys has removed all Edwards Group deposits except in the headwater regions. The meandering channels of these streams are incised, and intersect the subterranean systems which drain the perched valley floors. The Blanco drainage is considerably smaller than the Guadalupe drainage, and the processes of entrenchment and the development of subsurface

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drainages are correspondingly less advanced. Most of the subsurface drainage of the upper Blanco valley appears to be diffuse, with discharge occurring via numbers of small springs along the river channel; the lower portion of the valley shows moderate development of sinkholes, but the river channel is not so deeply incised as to intersect the major solutional passages. This lower valley system apparently discharges through Jacob's Well, a deep, water-filled solution tunnel on a tributary of the Blanco at the downstream margin of the Blanco valley.

The Guadalupe River valley represents a mature combination of surface and subsurface drainages. As is repeatedly noted in the regional hydrologic literature (see George, 1952; Petitt and George, 1956; Garza, 1962), the Guadalupe is alone among the plateau drainages to the south and west of the Colorado River in contributing no water to the Balcones Aquifer; it recaptures the subsurface drainage of its valley, and flows at or near the level of the water table from the head of this valley through the entire transect of the Balcones Fault Zone. The river channel forms deeply incised meanders from the fault zone inland to the eastern edge of Kerr County, straightening and rising to the valley floor level thereafter as it becomes enclosed in divide areas formed of Edwards Group limestones. The river maintains permanent flow as far upstream as the horizon of the basal Fort Terrett Formation.

Regional lithology forms an extremely important aspect

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of the development of the Guadalupe valley. Throughout Kendall County and northern Comal County west of Spring Branch the base of the local water table is formed by the Hensel Formation on which the river flows. Subsurface drainages are highly developed in the overlying basal unit of the lower Glen Rose limestone, with networks of sinkholes forming local systems which discharge into the river or its tributaries as stream caves at the Hensel-Glen Rose contact (see Chapter VI). Entrenchment and subsurface system development apparently occurred simultaneously, as judged from two lines of evidence. No stream caves are known to cross the bed of the river or its major tributaries, nor do any caves display contralateral equivalents which might indicate the presence of such systems in the past. Further, it appears that most of the enlargement of these subsurface drainages postdates their capture by entrenchment. Many of the stream caves of the region bifurcate where intersected, and the branches are subequal in size; since these distributaries are discharge structures which must postdate intersection, the relation of main channel diameter minus distributary diameter is an estimate of the size of the main channel prior to intersection. This estimated size averages about one third of the present size of the caves. These estimates are concordant with the expectations of the general model, in that solution of limestones is partly dependent on the flow rate of the dissolving agent, and that flow rate is partly a function of the discharge potential of the end of the subsurface sys-

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tem; discharge potential increases greatly once the solutional channel is breached by a surface drainage. It is important to note that intact subterranean systems develop more slowly than do intersected ones, and thus that it is incorrect to assume that a small intact solutional channel is necessarily a youthful one, or that a large intersected cave is necessarily older than a smaller intact cave.

A further correlate of this general model of the development of surface-subsurface relationships is that the subterranean drainages should develop from the river channel outwards and extend no farther than the crests of the surface divides. George (1952) reports that in Comal County wells drilled into lower Glen Rose strata have a good chance of finding adequate water supplies only where upper Glen Rose strata are thin or absent; i.e., only on the valley floor, and especially in the central zone of the valley. Wells drilled into the lower Glen Rose from positions on the thick upper Glen Rose deposits of the divides rarely if ever produce usable quantities of water (George, 1952).

Because the gradient of the Guadalupe River is slightly steeper than the regional dip of the strata, the Hensel Formation is transected near Spring Branch, Comal County, and the river is entrenched into the upper part of the Cow Creek Limestone. Here the small flat valley of Rebecca Creek is developed on the Cow Creek surface, and is drained by a subsurface system very similar to those of the adjacent lower Glen Rose deposits; this system discharges via a small

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stream cave near the junction of Rebecca Creek and the Guadalupe River. Immediately downstream the short throw of the Spring Branch Fault restores the Hensel-based Glen Rose aquifer system of the main Guadalupe valley. This lower segment shows comparable development of subsurface drainages in the few kilometers of its extent inland to the Balcones Fault Zone.

Drainages to the north of the Blanco River either predate the plateau and transect it with little attendant development of subsurface features (the Colorado River), or have developed without the influence of the Balcones Fault Zone in an area in which the Edwards Group limestones are comparatively thin, and in which the outcrop of the Llano Uplift plays a dominant erosional role (the San Gabriel and Lampasas Rivers). The development of these systems does not conform to the pattern of those of the main body of the plateau, bearing closer similarities to the ontogent of non-karstic drainages, and is not considered important enough to discuss in this context.

In summary, a general model of the erosional and solutional development of drainages on the Edwards Plateau can be constructed from an examination of the existing drainages, using the volume of water transported as the independent variable (which is actually a composite effect of rainfall and basin size), and holding the influences of lithology and the Balcones Fault Zone constant. Having developed dendritic drainage patterns on the Edwards Group limestone surface,

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drainages downcut narrow valleys to the basal Fort Terrett Formation then stabilize while lateral development of broad interior valleys takes place on the surface of the Glen Rose limestones, mediated by undercutting and collapse of the overlying Edwards, and by the saturation of the valley floor by discharge from the main plateau aquifer. With the reduction of water-bearing and bed load-producing rocks on the lower divides stream gradients fall and the entrenchment of river channels begins, accompanied by the development of efficient subterranean tributaries where regional lithology permits. This stage may be relatively stable, and is the most mature condition displayed on the present plateau. It is suggested that the development of drainages on the maturely eroded eastern limb of the plateau has followed this course, and that in time the drainages of the western limb will reach the condition characteristic of the Blanco and Guadalupe drainages at present.

The correlation of these erosional stages with geologic time is a matter of further abstraction from the available evidence, which consists solely of the ages, compositions and areal extents of clastic deposits on the Gulf Coastal Plain. One possible interpretation of the origin of these clastics of the Miocene Oakville and Fleming Formations, the Pliocene Goliad Formation, the Plio-Pleistocene Uvalde Gravel, and the early Pleistocene Willis Formation is as follows. The Oakville and Fleming Formations are restricted in occurrence to the coastal plain to the east of the Ed-

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wards Plateau (Weeks, 1945b), thinning to the southwest: as previously noted the chert in these deposits could be derived only from erosion of massive amounts of Edwards Group limestones; the only identified Cretaceous fossil present is an index species of the lower Del Rio Clay. These deposits unequivocally demonstrate the development of large drainages on upper Comanche Series rocks of the eastern limb of the plateau during the Miocene (see also Woodruff, 1977); if the general model is valid it appears that canyons comparable to those of the western limb of the present plateau were forming in the ancestral drainages of the eastern limb during early and middle Miocene times. This process continued during the deposition of the very thick overlying Fleming Formation of late Miocene age, which extends somewhat farther to the southwest along the Gulf Coastal Plain than does the Oakville Formation (Weeks, 1945b; Geol. Atlas of Texas, 1974). Because the Miocene deposits of the Gulf Coastal Plain farther to the west contain no chert or reworked Cretaceous fossils an interpretation seems tenable that the Devils River and Edwards Group limestones of the western limb of the plateau were not exposed until post-Miocene times, although the southwestward extension of the Fleming Formation suggests that the region of the present Medina drainage was so exposed by the end of the Miocene, an interpretation supported by data presented on the development of the Balcones Aquifer by Abbott (1974; 1975) and Mench (1978).

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The overlying fossil- and chert-bearing Goliad Formation of early to middle Pliocene age extends from the Brazos drainage to the Rio Grande (Weeks, 1945a), and indicates the westward progression of the exposure of Devils River and Edwards Group limestones, probably to include the remainder of the southern Edwards Plateau. This southwestward progression of gravel deposits is continued in the Plio-Pleistocene Uvalde Gravel, a broad sheetlike deposit whose remains are most extensive on the upper Gulf Coastal Plain immediately below the western limb of the plateau (Weeks, 1945a, Fig. 1), reducing to very local deposits in the region of San Antonio and disappearing to the northeast. Deposits north of Comal County referred to the Uvalde Gravel by Weeks (1945a) are now considered to be of Pleistocene or recent origin (Geol. Atlas of Texas, 1974). Considerable caution must be exercised in interpreting the source of the Uvalde Gravel, as Byrd (1971) has shown that it consists in part of reworked clastics from the Ogallala Formation to the northwest. The Uvalde of the Coastal Plain may well be derived both from the Miocene Ogallala, and from later erosion of siliceous interclasts from the Edwards of headwater drainages. The inland gravel deposits seem to represent the period of initial canyon formation and the onset of the lateral expansion of interior valleys. Once these valleys were established and the stream gradients stabilized on the saturated upper Glen Rose surface the capacity of the rivers to transport large clastics diminished greatly, resulting in the thinning

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and disappearance of gravel deposits downstream on the Gulf Coastal Plain. Such insoluble materials as are normally carried by the streams of this and later stages are of small size, and their origin may pass unrecognized. The Pleistocene Willis Formation, of broad areal extent on the upper Gulf Coastal Plain, appears to represent one interval of increased erosional activity and transportation capacity in the drainages of the eastern plateau.

Thus the evidence of the Uvalde Gravel so favored by biologists is seen to represent one of the most recent deposits recording erosional activity on the Edwards Plateau, rather than one of the earliest. Further, while some of the components of Uvalde Gravel do represent an initial exposure of Edwards Group and Devils River limestones, this occurred on the western limb of the plateau long after such exposure is documented on the eastern limb. The common error has been in the assumption that little temporal variability existed in the degree of erosional activity across the entire Edwards Plateau, leading to the misapplication of the dating appropriate to the development of the Devils, Nueces, Frio and Sabinal Rivers to the development of the eastern plateau drainages. The Edwards Plateau has been an elevated physiographic unit since at least the early Tertiary, and has presented a dissected, hard carbonate landscape since early or middle Miocene.

Development of the Balcones Aquifer

No account of the geomorophology of the Edwards Plateau

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is adequate without a consideration of the structure of the Balcones Fault Zone and the extensive aquifer it contains. Much of the investigation of the geology of the plateau has been directly concerned with the hydrology of this economically important aquifer, and the literature is correspondingly extensive, though highly repetitious. Only a review of the broader aspects of ths structure and hydrologic function of this complex system is attempted here. Several general reviews of the Balcones Aquifer are available, the most complete being those of Garza (1962; 1966), the U.S. Army Corps of Engineers (1964), Maclay (1974) and Abbott (1975); in addition, considerable detailed information is to be found in the county-level analyses of the U. S. Geological Survey and the Texas Water Development Board (Arnow, 1959; Bennett and Sayre, 1962; DeCook, 1960; George, 1952; Holt, 1959; Petitt and George, 1956; Sayre, 1936; Reeves and Small, 1973; and Welder and Reeves, 1962).

The Balcones Fault Zone extends from Bell County south through Bexar County and west to Val Verde County, with the greatest displacements (whether on single faults or in total) in Comal and Bexar Counties across the axis of the San Marcos Platform. The surface expression of the fault zone ranges from about 5 to 40 km in width, in cross-section usually consisting of 2-5 major faults of 10-60 km in length arrayed in a parallel fashion, and a larger number of minor faults less nearly parallel to the main trend. All of the major and most of the minor faults are downthrown on their coastal

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face, though a few short faults dip in the opposite direction (Weeks, 1945c). The results of this activity are the downward displacement and shattering of the massive Devils River, Edwards Group and Georgetown Limestones along the margin of the Edwards Plateau, together with the displacement of the underlying Glen Rose Formation and the overlying Del Rio Clay. The latter formations are resistant to solution by virtue of their high clastic contents, and serve as vertical boundaries to the Balcones Aquifer developed within the bracketed formations. Solutional development within the aquifer is facilitated by three factors: the availability of large volumes of water captured by the Devils River and Edwards Group outcrops of the inland margin of the fault zone where transected by the plateau drainages between the Devils and Colorado Rivers (excepting the Guadalupe River); the predominantly clastic-free carbonate lithologies of the depressed Devils River and Edwards Group limestones; and the mechanical fragmentation of these units in the fault zone. The result is an arcuate band of extremely porous rocks along the coastal margin of the Edwards Plateau which captures, transports and releases immense quantities of water.

Much of the porosity in the Balcones Aquifer is related to the original distribution and post-uplift modification of dolomites and dolomitic limestones. As detailed by Rodda, et al (1966) and Fisher and Rodda (1967), dolomitized beds are abundant in the upper Fort Terrett Formation and throughout the overlying Segovia Formation around the periphery of the

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broad Kirschberg Lagoon of late Fredericksburg time. The southeastern margin of this shallow evaporite basin lay across the axis of the Balcones Fault Zone in the region of the San Marcos Arch, the same area in which the Balcones Aquifer is best developed at present. Abbott (1974) has documented a diagenetic reversion of dolomite to limestone within the confines of the Balcones Aquifer, which appears to be the result of high flushing rates within the aquifer by water of high Ca/Mg ratios. The calcitization of the dolomitic beds within the region of the Balcones Aquifer has resulted in recrystallization of the calcite into a coarser matrix (Mench, 1978); this in turn has improved solution rates within the dedolomitized beds by increasing their porosity (Abbott, 1975).

Many of the larger channels within the Balcones Aquifer are developed by solutional enlargement of joints and fractures in the dedolomitized beds. Continuing post-Miocene movement among the component blocks of the Balcones Fault Zone has elevated inland portions of the system above the level of the present aquifer, permitting direct investigation of the structure of the major passages. Caves such as Wonder Cave (San Marcos) and Airman's Cave (Austin) are probably typical of the still-active portions of the Balcones Aquifer (Russell, 1975; 1976). Both exhibit joint control of passage orientation, and bedding control of horizontal development, with most of the passages lying in dedolomitized beds. Airman's Cave is essentially planar, but Wonder Cave

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is developed on three superposed levels linked by shallow collapse pits. Both caves would provide free-flow conditions for large amounts of groundwater. Equilibration rates for water-level changes within the Balcones Aquifer are typically very high, further indicating the existence of continuous large passages throughout the system, particularly in the vicinity of the large springs through which the aquifer discharges (Russell, 1976).

The average annual recharge to the entire Balcones Aquifer is estimated to be in excess of 8.0×10^8 cubic meters (calculated from data in Garza, 1962, and Brune, 1975). Prior to agricultural and industrial development of the region this recharge was balanced by discharge from 9 major springs (and a few smaller springs) along the fault zone from Bell County south and west to Val Verde County; from northeast to southwest these are Salado, Barton, San Marcos, Comal, San Antonio and San Pedro, Leona, Las Moras, San Felipe and Goodenough Springs (Brune, 1975).

The Balcones Aquifer is subdivided into four hydrologic units which are partially independent of one another: a little-studied western unit (Goodenough, San Felipe and Las Moras Springs); the major, well-studied central unit (Leona, San Antonio and San Pedro, Comal, and San Marcos Springs); and two poorly understood northern units (Barton Springs; Salado Springs) divided by the channel of the Colorado River. The northernmost unit is probably quite small, since the drainages north of the Colorado River (excepting Salado

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Creek) are excavated below the Edwards Group limestones (Rodda, et al, 1966; Plate 1) and thus contribute little or no water to the subsurface.

The central unit of the aquifer is demarcated by groundwater divides in central Kinney County and northeastern Hays County (Garza, 1962, Plates 1 and 2). The central unit is bounded on the north by steep hydrologic gradients in the exposed Devils River and Edwards Group limestones of the fault zone where recharge occurs. Local hydrology is extremely complex in this gravity-flow or water table segment of the aquifer, being mediated by the variable development of solutional openings in the fractured strata. The main aquifer supplied by this recharge surface is primarily under artesian conditions (confined by the Glen Rose and Del Rio Formations, and behaves as a hydrologic unit throughout, indicative of extensive interconnection among large solutional passages. The western and northern units of the Balcones Aquifer seems to operate mostly as gravity-flow aquifers of relatively low to moderate porosity.

The Balcones Aquifer probably first developed in the region of the San Marcos Platform (in Hays, Comal and Bexar Counties) where the total displacement of the fault zone has been the greatest, and extended northward and westward as the plateau drainages developed and the Devils River and Edwards Group limestones of the fault zone were exposed by the development of the ancestral plateau drainages. From the previous discussion of erosional history it seems likely

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that the aquifers supplying Barton, San Marcos, Comal and perhaps San Antonio and San Pedro Springs began development in mid-Miocene times (Abbott, 1975; Mench, 1978), with the western segment of the central aquifer unit developing through late Miocene and early Pliocene times; the western unit of the aquifer probably developed in late Pliocene or early Pleistocene. The segment of the Balcones Aquifer north of the Colorado River is probably younger than that to the south, and is perhaps of Pliocene or Pleistocene age.

Conclusion

Considering its great areal extent, the Edwards Plateau remains a rather simple geomorphic entity: a Cretaceous carbonate shelf broken along the axis of the Ouachita trend by the development of the Gulf Coast geosyncline during early and middle Tertiary times and stripped of its Upper Cretaceous deposits to expose the hard Lower Cretaceous limestones which define its present form. Since the middle Miocene erosional and solutional processes have differentiated a pair of surface and subsurface drainage patterns on the plateau and its coastward margin in a general east-to-west progression, consisting of an aquifer on the plateau surface which maintains base flow in the plateau drainages, and an aquifer supplied by these drainages in the marginal fault zone which discharges via large springs independent of the basins of the plateau drainages. This cleanly defined geomorphic unit has preserved considerable stability in mesic,

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aquatic and subterranean environments in a region of high faunal diversity and interchange during late Tertiary and Quaternary times and this role is reflected in the diverse faunal composition of the present Edwards Plateau (Blair, 1950; Remington, 1968; Mitchell and Reddell, 1971).

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CHAPTER III

A DISTRIBUTIONAL ANALYSIS OF EPIGEAN POPULATIONS OF THE TEXAS *EURYCEA*

Introduction

By virtue of its geographic location and geologic characteristics the Edwards Plateau of central Texas stands as a center of endemism and a region of relict populations for plants (Correll and Johnston, 1970) and animals (Blair, 1950; Remington, 1968; Mitchell and Reddell, 1971) derived from southeastern, neotropical and southwestern regions. The extensive flat-lying limestone strata of the Plateau have been moderately dissected by a series of shallow rivers radiating from the high and level northwestern sector; along the valleys of these rivers mesic floral and faunal elements interdigitate with the arid-adapted fauna and flora of the rocky, well-drained divides. The persistence of mesic relicts is largely due to the role of the limestones of the Plateau as a major aquifer. The groundwater of the Plateau is discharged by numerous springs in headwater canyons, and along the broad curve of the Balcones Fault Zone, which sharply delimits the uplands of the Plateau from the coastal plain to the east and south.

The headwater and fault zone springs of the Edwards Plateau and their associated subterranean drainages are inhabited by relict populations of hemidactyliine plethodontid salamanders of the genera *Eurycea* and *Typhlomolge*.

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These exclusively aquatic and generally paedogenetic salamanders have proven to be sufficiently widespread and diverse that an analysis of their distribution is a necessary preliminary for a detailed treatment of the evolution of this group as a whole. The distribution of the highly specialized troglobite Typhlomolge rathbuni has been clarified recently by Russell (1976) and Longley (1978); an analysis of the occurrence of troglobitic populations of Eurycea is presented in Chapter IV.

The present chapter details the distribution of epigean (surface dwelling) populations of Eurycea neotenes, and seeks to identify the determinants of this distribution in the geologic structure and hydrologic characteristics of the Plateau. The analysis is composed of several parts. Following a general treatment of the known distribution of epigean populations three interrelated aspects of this distribution are detailed and examined: (1) the restriction of populations to the immediate vicinity of springs; (2) differences in the degree of temporal reliability of springs; and (3) geologic and topographic correlates of spring reliability. The latter correlates are then employed in a comprehensive survey of the Edwards Plateau, with two objectives: first, to estimate the number and density of populations of E. neotenes within the known range; and second, to evaluate the possibility that populations occur beyond the limits of the presently known distribution.

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Materials and Methods

Field work was conducted in June, 1969; June and July, 1970; July and August, 1971; and from June through September in 1973 and 1974. A total of 3700 specimens of E. neotenes representing 85 epigean populations was collected during this period, augmented by about 700 specimens representing at least 10 additional localities borrowed from other collections. The localities, specimen numbers and repositories of these series are listed in Appendix I . Detailed field notes are on file in the Museum of Vertebrate Zoology, University of California, Berkeley.

Locality and topographic data were taken from the 7½' maps of the U.S. Geological Survey; these maps now provide essentially complete coverage of the southern Edwards Plateau. In addition to data for springs which were visited in the course of field studies, topographic information was collected for all other springs indicated on 468 of the 478 7½' maps (10 quadrangles not mapped) within the following area (see Fig. 7): from 30° 45' 00" N, 101° 37' 30" W due east to 99° 15' 00" W; thence stepwise northeast (increments 7½' latitude, 15' longitude) to 31° 22' 30" N, 98° 15' 00" W; thence due east to 97° 15' 00" W; thence due south to 30° 22' 30" N; thence stepwise southwest (in 7½x15' increments) to 29° 07' 30" N, 98° 30' 00" W; thence due west to to 100° 52' 30"; thence northwest along the United States - Mexican border to 29° 45' 00" N, 101° 37' 30" W; thence due north to 30° 45' 00", completing the polygon. Full data from

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Figure 7. Geography of the southern Edwards Plateau of central Texas. County names within the Plateau as limited in this work are indicated, and the margins of the Balcones Fault Zone and the Llano Uplift are marked by hatchured lines. A continuous line marks the boundaries of the polygon surveyed on topographic maps (see text).

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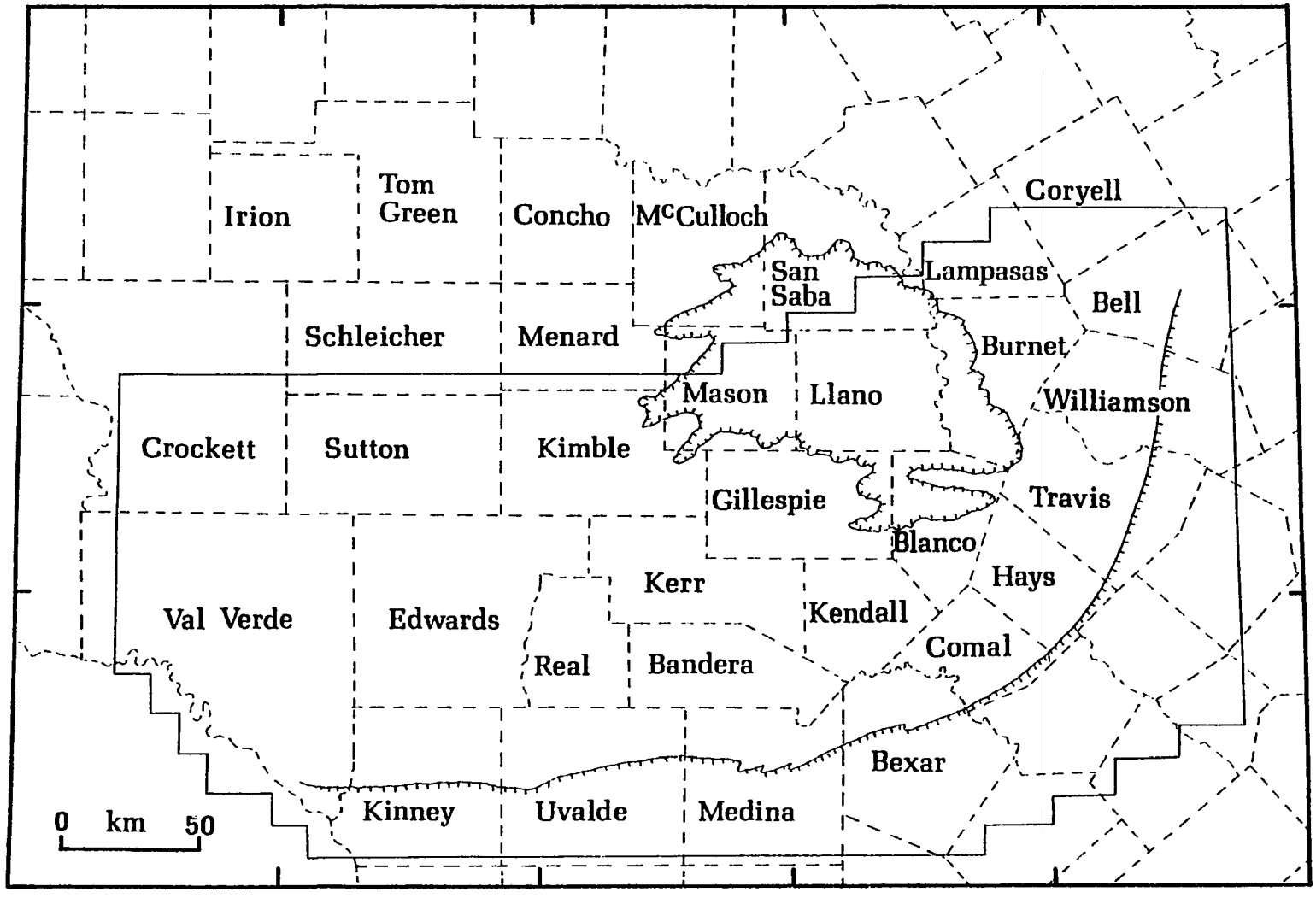

this survey are available from the author. This region encompasses the Balcones Fault Zone and the adjacent Gulf Coastal Plain as well as the major part of the Edwards Plateau and Llano Uplift. The known distribution of the Texas Eurycea comprises about 127 7½' quadrangles roughly centered within this polygon, surrounded by a broad zone in which members of the genus are unknown to occur.

Results and Discussion

Distribution of Epigean Populations

Distributional information, summarized and expanded by Baker (1961), comprises much of the early literature concerning the Texas Eurycea; relatively few localities have been reported in recent years. A general outline of the range of epigean populations is given by Sweet (1976; 1977 [Chapter V]), but localities of collections are not indicated for the major portion of the suggested distribution. Figure 8 conveys this information; the precise locations of 95 of the 102 populations shown are presented in Appendix I . A few records based on museum specimens or literature reports cannot be precisely located, and most of these are omitted from the map (none is believed to be extralimital to the indicated range); the available information on these localities comprises Appendix II. The considerable local differentiation observed among populations of the Texas Eurycea greatly reduces the value of samples with vague locality data.

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Figure 8. Distribution of epigean populations of *Eurycea* (chiefly *E. neotenes*) on the Edwards Plateau. Counties are outlined. Filled circles mark known populations; open circles denote springs potentially suitable for *E. neotenes* as discussed in the text. Dashed distributional boundaries indicate regions in which populations of *E. neotenes* are expected to occur. Localities marked are noted in Appendices I and II.

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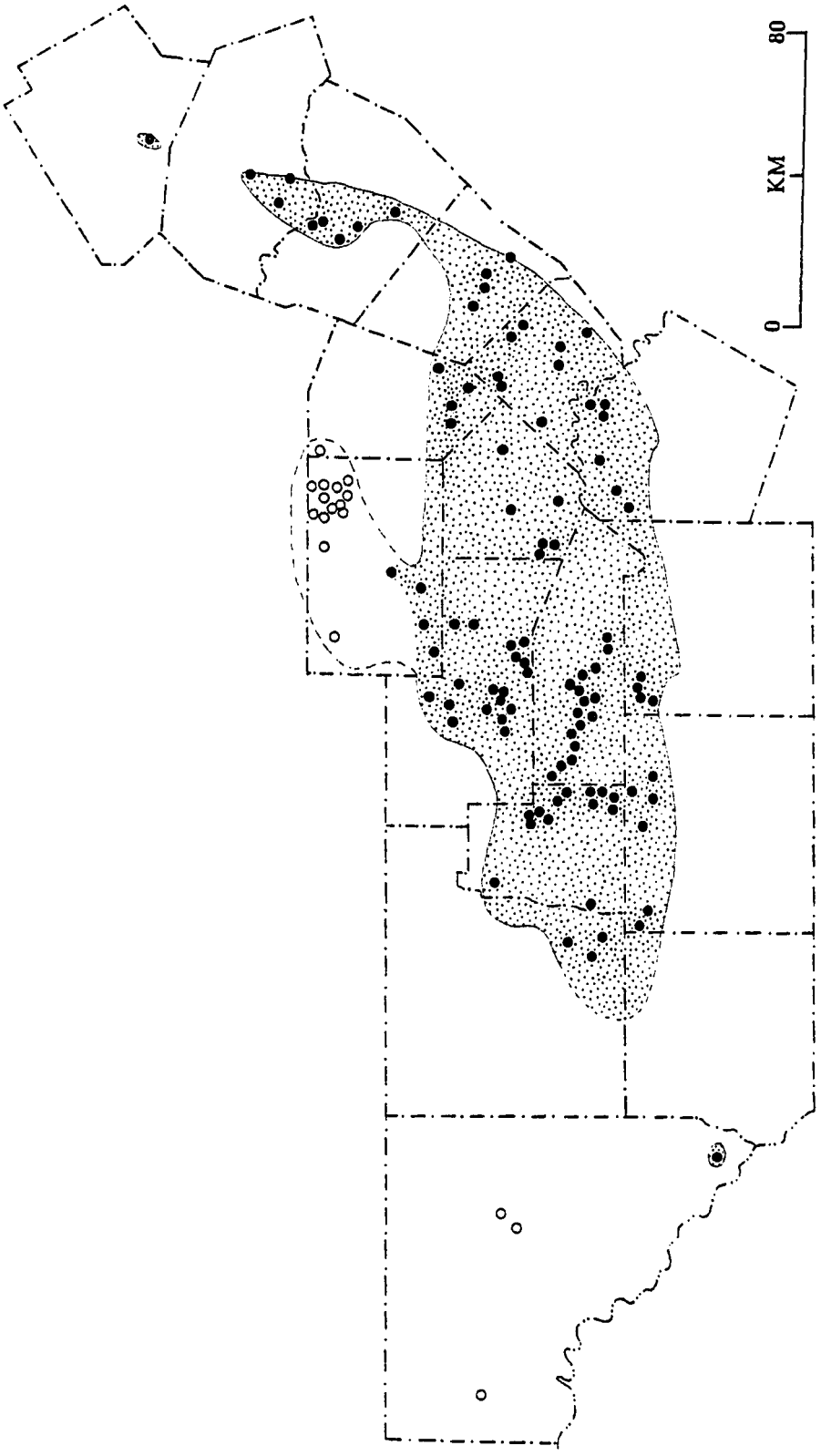

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From a comparison between Figure 8 of this chapter and Figure 1 of Chapter I it is apparent that populations of Eurycea neotenes are restricted to the dissected southeastern region of the Edwards Plateau, becoming more closely confined to its coastal margins in the northeastern and southwestern portions. Populations are most numerous in the rugged west-central part of the overall range in the region between the headwaters of the Guadalupe and Nueces rivers. Both the number of springs and the proportion of springs found to be inhabited by E. neotenes reach maximum values in this region, as discussed below, and it is the only area in which naturally metamorphosed individuals are known among these usually paedogenetic salamanders (Sweet, 1977 [Chapter V]).

As is evident in Figure 8, the Balcones Fault Zone is the limit to the distribution of E. neotenes. The rapid decline of the water-bearing strata of the Plateau into the subsurface coastward from the fault zone is the probable limiting factor. The very large reservoir underlying the fault zone and the sharp dichotomy between permeable and impermeable strata produced by faulting result in the emergence of several very large springs at widely separated points; small springs are relatively uncommon. Seven springs in the Balcones Fault Zone have average annual discharges in excess of 17,000 liters/second (Brune, 1975); from northeast to southwest these are Salado, Barton, San Marcos, Comal, San Antonio, Las Moras and San Felipe springs. Populations

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of Eurycea are presently known from all but San Antonio and Las Moras springs, both of which have been extensively altered by impoundment and heavy pumping from local wells. The salamanders inhabiting these large springs are frequently distinctive, tending to be more slender and of a more uniformly dark dorsal coloration than is usual among populations of E. neotenes on the Plateau proper. The population inhabiting San Marcos Springs has been described as Eurycea nana (Bishop, 1941), and is generally recognized as valid; the population which inhabits Comal Springs, some 27 km to the southwest, is very similar to E. nana and is probably conspecific (Sweet, in preparation). The Barton Springs population is distinctive and warrants nomenclatural recognition (Sweet, in preparation). The Salado and San Felipe springs populations are presently known from immature specimens whose taxonomic affinities are not determinable. Apart from the populations restricted to fault zone springs the remainder of the epigean populations on the Plateau are referable to Eurycea neotenes. One population in Hays County which has been previously accorded specific or subspecific status (Eurycea pterophila) is indistinguishable from E. neotenes (Sweet, 1978; Chapter VII).

A single Eurycea from a small eastern outlet of Salado Springs, Bell County, represents the northeastern limit of the known distribution of the Texas Eurycea. Three localities are known in Williamson County, which adjoins Bell County to the south. Single specimens of E. neotenes have

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been collected in a small fault zone spring in Georgetown, and in a similar situation in the town of Round Rock. A series of 53 E. neotenes is available from Krienke Spring, about 6 km NW of Round Rock (this population no longer exists, the spring having been incorporated into a limestone quarry in the early 1960's). Apart from Krienke Spring, populations of E. neotenes seem to be very small and of uncommon occurrence in Bell and Williamson counties. The Georgetown site has been visited on seven occasions, Salado Springs on four occasions, and the Round Rock site twice without observing additional salamanders. Nine other springs in this area have been searched between one and three times each without success.

In southern Williamson and northern Travis counties the zone of outcrop of the resistant Edwards Group limestones associated with the Plateau margin expands to form a small upland termed the Jollyville Plateau. The deep canyon of the Colorado River isolates this area from the main body of the Edwards Plateau to the south and west, apparently resulting in the observed high percentage of endemic species of troglobitic invertebrates in the caves of the Jollyville Plateau (Mitchell and Reddell, 1971). Four epigean populations of E. neotenes are known from the margins of the Jollyville Plateau, and others are reported but not confirmed by collections.

There is a hiatus in the known distribution of E. neotenes in the region between the Colorado River in central

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Travis County and the Blanco River drainage of central Hays County (Fig. 8) which is probably real, resulting from the paucity of springs owing to unfavorable stratigraphic conditions (Chapter II). Populations of E. neotenes become numerous to the south and west of central Hays County where outcrops of Edwards Group limestones and the deep canyon of the Guadalupe River provide hydrologically stable conditions.

The northern limits of the presently known range of the Texas Eurycea correspond with the headwaters of the Blanco River in Blanco and Kendall counties, and the southwestern tributaries of the Pedernales River in southern Gillespie County. In the latter drainage populations of E. neotenes occur along the tributaries of Wolf Creek (Trough Springs) and White Oak Creek (Cottonwood Spring), and in the town of Fredericksburg, Gillespie County. One museum specimen (Appendix II) has as locality data "N Fredericksburg Wolf Creek;" these data are contradictory, because the only Wolf Creek in the area lies south of Fredericksburg. This is the probable locality of the specimen, though the existence of a population in the northern tributaries of the Pedernales drainage north of Fredericksburg cannot be disproven. No populations were found in a search of four springs in this region, but it is likely that they exist on the basis of the analysis developed below.

Westward from the Guadalupe-Pedernales divide numerous populations of E. neotenes occupy the headwater springs of the Guadalupe, Medina, Sabinal, Frio and Nueces rivers in a

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zone extending from eastern Kerr County into southeastern Edwards County. However, E. neotenes apparently does not occur in the southern tributaries of the Llano drainage immediately to the north. The divide which separates the Llano drainage from those to the south is broad in Edwards and Kerr counties, becoming very narrow in Gillespie County to the east. As indicated below E. neotenes may be found to occur in northeastern Gillespie County.

The western limits of abundant populations of E. neotenes lie in the Nueces River drainage of Real and southeastern Edwards counties. Farther west suitable spring habitats appear to diminish sharply, and those which exist are now heavily modified by man. Eurycea neotenes is very likely to occur beyond the limits of the presently known distribution in a small area of southern Edwards and northern Kinney counties, as shown in Figure .

The westernmost known epigean population of the Texas Eurycea is disjunct (Fig. 8), inhabiting the small southwestern outlet of San Felipe Springs about 2 km NE of Del Rio, Val Verde County. Two immature specimens were collected on the third of five visits to this complex of springs associated with the western terminus of the Balcones Fault Zone. Intensive sampling has failed to produce additional specimens, and it is likely that the population is in part subterranean, as is the case at Barton Springs in Travis County (see Chapter IV).

The apparent absence of epigean populations of Eurycea

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along the Balcones Fault Zone in Medina, Uvalde and Kinney counties probably reflects the low topography and general scarcity of springs characteristic of the lower reaches of the divides separating the western Plateau drainages as discussed in Chapter II.

Several general correlates of the known distribution of epigean populations of the Texas Eurycea can be drawn from the information at hand, including: (1) the restriction of populations to regions of limestone outcrop; (2) the virtual restriction of populations to the immediate vicinity of springs; (3) the role of the Balcones Fault Zone in providing suitable aquatic habitats in otherwise marginal areas; and (4) an apparent correlation between the degree of regional topographic relief and the abundance of populations. All of these correlates may be combined into a general statement that the existence of reliable springs determines the present distribution of epigean populations of the Texas Eurycea. Evidence presented below expands this general conclusion in terms of water temperatures, the nature of the geologic control of the location and reliability of springs, and the influence of local topography on the relative reliability of springs on the Plateau proper.

Restriction to Springs

Field experience indicates that epigean populations of Eurycea neotenes are restricted to the vicinity of springs, at least during the summer months (comparable data are not

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available for other periods). While occasional individuals may be found in excess of 25 m from any evident spring, each of the 85 epigean populations located in the course of field work was closely associated with the outflow of one to several springs. This association may be due to the combination of favorable conditions offered by these sites, including: the prevention of siltation in the gravel beds in which most populations occur; the maximized reliability of the water source in this region of intermittent drainages; and the thermal stability characteristic of springs. Siltation is common in the low-gradient streams of the Edwards Plateau, and calcareous deposits frequently produce a pavement-like bed in intermittent streams. Both conditions eliminate the interstices inhabited by salamanders; neither is of common occurrence in proximity to springs. As a general rule the groundwater on the Plateau proper is not saturated with calcium carbonate, and thus precipitation of calcium deposits does not occur unless significant evaporation takes place on the surface. The importance of reliable water sources to the occurrence of wholly aquatic salamanders is self-evident. The thermal stability of the spring environment may be of critical importance during the summer months, when water temperatures in the exposed shallow streambeds of the Plateau are frequently in excess of 30° C (Fig. 9; Goines, 1967; Brune, 1975). Slight geographic variation is evident, with temperatures tending to increase from 18-19° C to 19-20° C with decreasing latitude. Also,

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Figure 9. Comparison of the ranges of annual fluctuations in temperature in a typical Edwards Plateau stream (stipple) and in a large number of springs on the Plateau proper (black). Stream values are for the Blanco River at Wimberley, Hays County, between 1950 and 1966 (Goines, 1967); spring temperature data derive from sites throughout the Plateau as reported in publications of the Texas Water Development Board.

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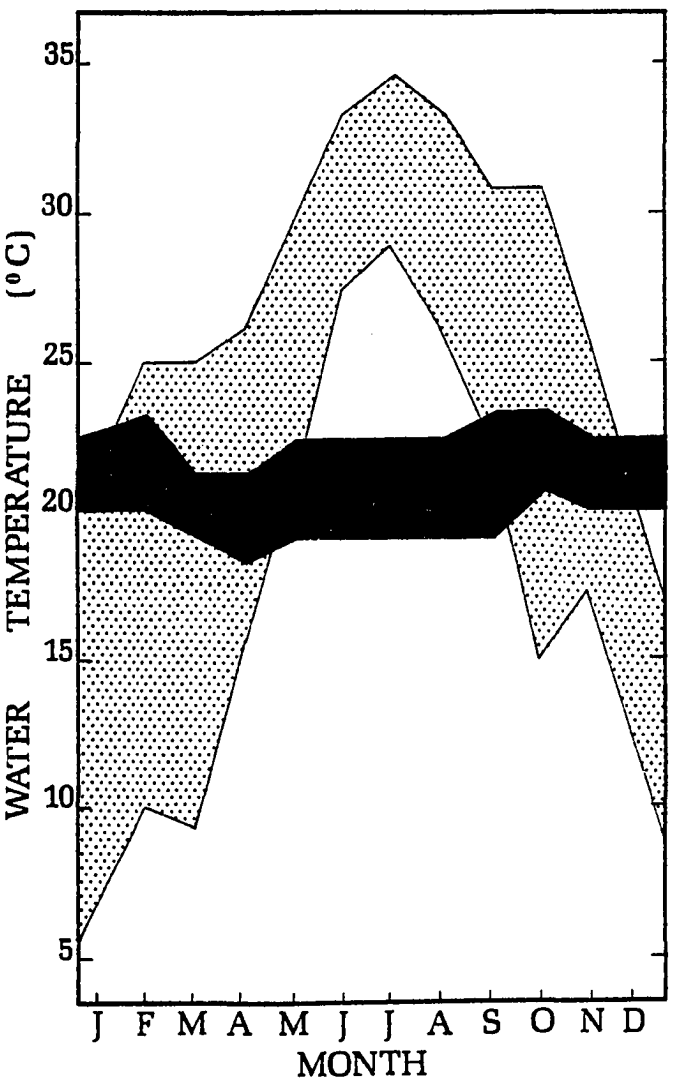

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the deep circulating water discharged by the artesian springs of the Balcones Fault Zone is typically 1-2° C warmer than that of adjacent water-table springs.

Hemidactyliine salamanders are generally associated with cool temperatures (Brattstrom, 1963; Spotila, 1972), with the upper limits of their preferred thermal range roughly coincident with spring temperatures on the Plateau. As indicated by Figure 9, it should be emphasized that these are the coolest waters consistently available during the period from May to September.

The distribution of water temperatures at 34 sites where one or more specimens of E. neotenes was collected is shown in Figure 10. Most data points represent discrete spring populations, save for the higher temperature values which derive from three collections made downstream from springs, which involve few individuals. While downstream habitats were not examined as thoroughly as were spring outlets, salamanders were regularly sought while approaching springs, and the observed temperature association with occurrence is felt to be real. Much of the dispersion seen in Figure 10 owes to local variation in spring temperatures rather than reflecting an occurrence of specimens in downstream areas; even so, about 87% of the 675 specimens with temperature data were collected in the 18-21° C range.

An instructive example of the correlation of the occurrence of E. neotenes with cool water temperatures was noted on 4 September 1973 on the Clear Fork of Cibolo Creek in

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Figure 10. Frequency distribution of water temperatures at 34 sites of collection of one or more individuals of *Eurycea neotenes*. Numbers above each column indicate total numbers of individuals collected in each temperature interval.

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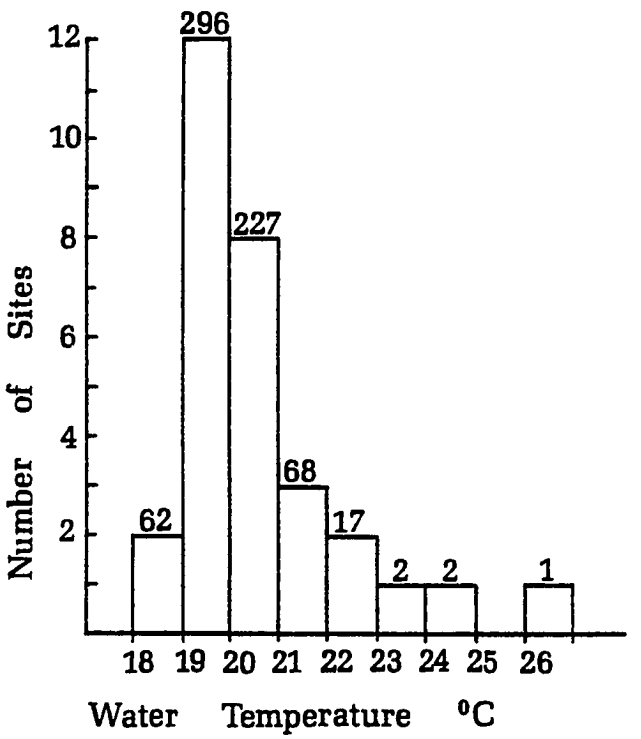

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northeastern Bexar County. Water temperatures of 27-30° C were recorded during an unsuccessful search of this shallow, gravel-bottomed stream; eventually two small springs were located by a series of thermometer transects across the streambed near a small fault noted in the canyon wall. By dredging the gravel from the streambed at these points a series of 85 E. neotenes was collected within a radius of about one half meter from each of the submerged spring exits. Salamanders which escaped capture were observed to attempt to return to the vicinity of the springs before burrowing into the substrate.

Geologic Correlates of Spring Location and Reliability

The limestones of the Edwards Plateau are not uniform with respect to their abilities to store and transmit water. Only one stratum with broad surface exposure consistently carries substantial amounts of water, to the extent that springs occur in nearly every canyon transecting the contact of this layer with the underlying, relatively impervious strata. The base of this water-bearing layer is located from 8-12 m above the base of the Edwards Group limestones, and is termed the Burrowed Member of the Fort Terrett Formation (Rose, 1972; see Chapter II). It is comprised of a section of dense dolomite and dolomitic limestone 22-28 m thick whose lower portion is honeycombed with invertebrate burrows. The softer sediments filling these burrows have been leached away, and the overall porosity of

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the member has been enhanced by solutional enlargement of the burrows to form a zone of high storage capacity with rapid transmission characteristics (Rose, 1972). The Burrowed Member, and its (less well developed) lateral equivalent in the Devils River Limestone of the southwestern margin of the Plateau, are underlain by a zone of silty marl with abundant shell fragments and muddy nodules, variously termed the Walnut Clay, Comanche Peak Formation, or Basal Nodular Member (Rose, 1972). This contact occurs throughout the zone of Edwards Group outcrop indicated in Figure 5 of Chapter II, exclusive of the Balcones Fault Zone but including the Jollyville Plateau. The Basal Nodular Member (or its lateral equivalents) and the underlying upper Glen Rose Limestone consist of materials which are not easily dissolved or transported by groundwater; they thus form a relatively impervious lower limit to the aquifers of the Plateau proper.

The majority of springs inhabited by Eurycea neotenes on the Plateau proper are those developed in this lower region of the Edwards Group and Devils River limestones. Of the 154 springs examined in the course of field work, 140 occur on the Plateau proper, where the Edwards-Glen Rose contact is at least potentially exposed; the remainder are within the Balcones Fault Zone. Fully 85 of the 140 springs (61%) on the Plateau are located in the lower Fort Terrett and Devils River formations, and 66 (77%) of such springs were found to be inhabited by E. neotenes. In contrast, 18

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of the 55 springs (33%) which arise from other geologic horizons inland from the fault zone were found to be inhabited. The strata of origin of these 18 springs include: basal regions of the Cow Creek Limestone (2); basal lower Glen Rose Limestone (4); scattered horizons in the upper Glen Rose Limestone (8); and basal Segovia Formation (1). All but the last site are in regions of the Plateau surface where the Edwards Group limestones have been eroded away.

A more general anaylsis of the importance of the Edwards-Glen Rose contact to the location of springs is desirable, but is not feasible from topographic maps alone without direct field examination. An examination of quadrangles where this contact is exposed shows a nonrandom distribution of spring elevations; for example, in four quadrangles (Joy Hollow, Bee Cave Hollow, Jo Jan Van Camp and Owl Hollow) covering a region of headwater canyons in northwestern Real County elevations range from 490-730 m, with over 90% of the surface above 610 m. The elevations of 99 springs range from 534-647 m, with 87% located below 610 m. The basal units of the Fort Terrett Formation occur in a 43 m thick zone above the 555 m contour (Rose, 1972, Fig. 4), and contain 67% of the springs marked on the four quadrangles. The remaining springs arise in the upper Glen Rose Limestone (10) or in upper units of the Fort Terrett Formation (23).

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Topographic Correlates of Spring Reliability

In becoming restricted to aquatic environments as a consequence of paedogenesis, the Texas Eurycea have become dependent on the reliability of water sources. Springs provide the most reliable sources of water at the surface on the Edwatds Plateau, where aridity (free-surface evaporation exceeding precipitation by a factor of two or more) and the permeability of the land surface contribute to a scarcity of standing water and permanent streams fed by surface runoff.

Springs on the Edwards Plateau show a wide range in temporal reliability. Some, such as the major fault zone springs and those in canyons draining the main Plateau surface, rarely cease flowing. Others left above the present groundwater surface by erosional lowering of valleys, or in water-poor strata such as the upper Glen Rose Limestone,flow briefly after periods of heavy recharge but are otherwise dry. Most of the springs inhabited by E. neotenes lie between these extremes, and may cease flowing for short periods during dry seasons, requiring the resident population to withdraw temporarily into the subterranean spring channels. A discussion of the adaptations of the Texas Eurycea to the use of these underground refugia is presented in Chapter IV.

Salamander populations were apparently absent from a number of springs investigated in the field; many of these springs were noted to be in low-lying areas or high on divides in situations which might be expected to have unreliable recharge characteristics, and which might thus be prone

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to more frequent or prolonged failure than salamander populations could withstand. The locations of these springs are given in Appendix III. In the following section aspects of the hydrology of the Edwards Plateau supplemental to the discussion in Chapter II are briefly considered preliminary to the derivation of an index of spring reliability, which is then employed in an analysis of inhabited and uninhabited springs.

For an area of its size, the hydrology of the Edwards Plateau is relatively straightforward, involving two cycles of recharge, subterranean flow, and discharge via springs (Maclay, 1974). Precipitation on the Plateau surface is conducted underground through dolines, sinkholes, and fissures and contributes to an upland aquifer of irregular outline beneath the Plateau surface and its outlying divides. This aquifer is under gravity flow, water-table conditions, and discharges through springs at the headwaters of the marginal drainages and their tributaries, forming the base flows of these streams. Recharge on the Plateau surface ranges from about 9% of the average annual precipitation in the western counties (Reeves and Small, 1973) to about 3% in the eastern zone (Long, 1958; 1962; Bennett and Sayre, 1962; Reeves, 1969). A large percentage of the base flow of the Plateau streams reenters the subsurface through fissures and sinkholes in the streambeds in the process of crossing the band of Edwards outcrop in the Balcones Fault Zone, contributing to an extensive water-table and artesian aquifer along

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the coastal margin of the Plateau. The amount of flow so lost decreases in passing from the western to the eastern limb of the Plateau, and the Guadalupe and Colorado rivers contribute essentially no water to the fault zone aquifer (Chapter II). Each of the major fault zone springs derives its discharge from parts of the main fault zone aquifer, which is partially subdivided by low groundwater divides (Chapter II). The extensive recharge area and high storage capacity of the fault zone aquifer insures the fault zone springs against failure in all but the most severe droughts. Towards the end of the protracted drought of 1947-1957 rates of flow in all of the large fault zone springs declined, but only Comal Springs (June-November, 1956) and San Antonio Springs (1949-50; 1952-1957) ceased measurable flow (Brune, 1975).

In contrast to the very large aquifers which supply the fault zone springs, the aquifers of springs on the Plateau proper are of variable areal extent, and are often rather small. In general these aquifers correspond in size to the amount of adjacent and permeable land surface which is continously above the level of the local water table, artesian springs being rare or absent on the Plateau. This available recharge area tends to increase in passing upstream along the major drainages as a function of the decreasing degree of erosional dissection of the Plateau surface. Headwater springs of tributaries along the lower reaches of a drainage derive their water from the relatively small recharge sur-

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faces of isolated hills and narrow divides, whereas the springs at the headwaters of major drainages are supplied through a broad expanse of undissected Plateau surface.

The degree of temporal reliability of a spring is directly related to the capacity of the aquifer it discharges. To the extent that the size of an aquifer is a function of its recharge area, it should be possible to evaluate the reliability of a spring through some index of this recharge. Actual recharge potential is not easily determined, but a relative measure can be derived in the following way. Since the size of an aquifer is inversely related to the degree of local erosional dissection (as discussed in Chapter II), an index of this dissection can serve as an estimate of recharge area, and hence of spring reliability. In the present analysis, the maximum topographic relief within a one kilometer radius of a spring, excluding values for regions across canyons with lower elevations than the spring in question, is taken to be an index of erosional dissection. This measure probably provides a reasonable index of recharge area on the Plateau proper, where the flat-bedded and lithically uniform Edwards Group limestones erode to a comparable slope throughout. High relief values are associated with the headwaters of the major drainages and the narrow divides in the middle regions of the central drainages. Low values occur on the surface of the Plateau and along the valleys of the major streams, and outlying divides on the eastern and western limbs of the Plateau provide a range

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of intermediate values. Within the scope of the assumptions outlined above the measure of local topographic relief is an indirect index of the reliability of springs on the Plateau proper. This measure is invalid for those springs which discharge the fault zone aquifer, as local topographic relief exerts no influence on their recharge potential; nor is it valid for many of the springs along the lower reaches of rivers on the Plateau, particularly those lying very close to the river channel. These river-edge springs are resurgence points for water which has infiltrated the streambed, and are usually restricted to the upper Glen Rose Limestone and alluvial substrates. The assumptions made in this model are met by the following groups of springs: all those emerging from the Edwards Group limestones of the Plateau proper, the inner margin of the Balcones Fault Zone, and the Jollyville Plateau; and those springs emerging from the Glen Rose and older limestones other than riverside resurgences.

The data base for the analysis of spring reliability is illustrated in Figure 11. All springs examined in the field, with or without populations of Eurycea, are indicated on Figure 11; those springs indicated by horizontal lines were ignored analyzing local topographic relief, and those indicated by vertical lines were ignored in analyzing the effect of longitudinal position. The decline in topographic relief east of longitude 99° 30' W seen on Figure 11 corresponds to the zone in which the major rivers flow more or less eastward. Figure 11 also illustrates a tendency for uninhabited

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Figure 11. Scatter plot of springs inhabited by *Eurycea neotenes* (filled circles) and the springs lacking *E. neotenes* (open circles) with respect to maximum topographic relief within a one kilometer radius of each spring, and to longitudinal position. Circles with horizontal lines are excluded from Figure 12a, and circles with vertical lines are excluded from Figure 12b (see text).

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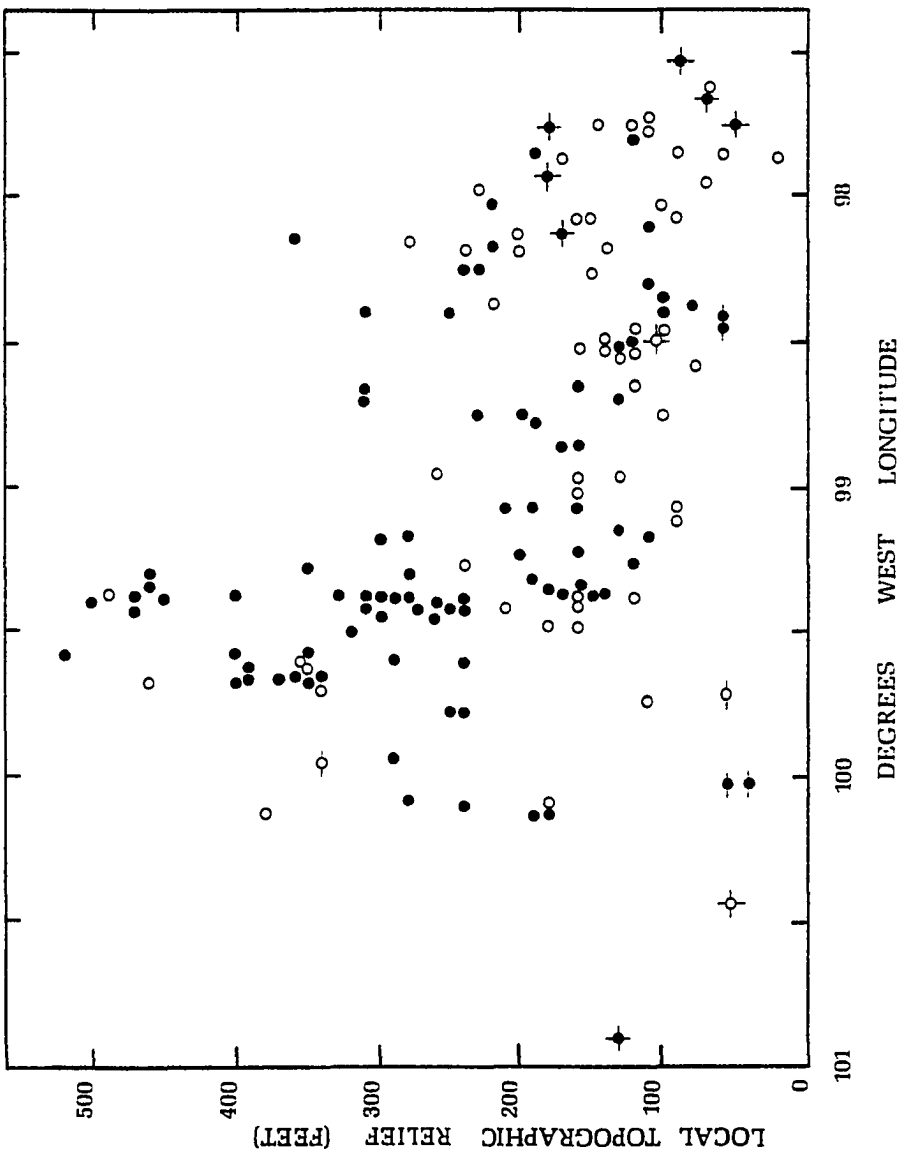

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springs to appear in the eastern region of low local topographic relief, and demonstrates the concentration of populations of E. neotenes in the west central portion of the overall range.

Figure 12 represents the projections of the data of Figure 11 (as restricted above) onto the reference axes of local topographic relief (Fig. 12a) and longitude (Fig. 12b). From Figure 12a it is apparent that the distribution of the 85 springs having populations of E. neotenes is offset towards higher local relief values than is the distribution of the 55 springs without E. neotenes. The two distributions are significantly different by Chi-square test (d.f. 4, X^2= 23.4; $p < 0.001$), indicating that the springs in the two observation classes are probably not subsets of the same group of springs with respect to local topographic relief. Within the sample analyzed springs lacking populations of E. neotenes have an average of 53.0 m of local relief, whereas those with E. neotenes average 76.2 m of relief. To the extent that local topographic relief is an index of spring reliability on the Plateau proper the importance of this criterion to the occurrence of populations of Eurycea neotenes is demonstrated.

Figure 12b indicates that the majority of springs apparently not inhabited by populations of E. neotenes are located in the eastern section of the Plateau; again the two distributions are significantly different (d.f. 5, X^2=24.9; $p < 0.001$). Fault zone springs were excluded from this anal-

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Figure 12. Projections of subsets of the data in Figure 11 on the reference axes. Figure 12a shows the distribution with respect to local topographic relief of springs inhabited by *Eurycea neotenes* (stipple) in comparison to those without populations of *E. neotenes* (open). Figure 12b shows the distribution of springs with and without populations of *E. neotenes* with respect to longitudinal position.

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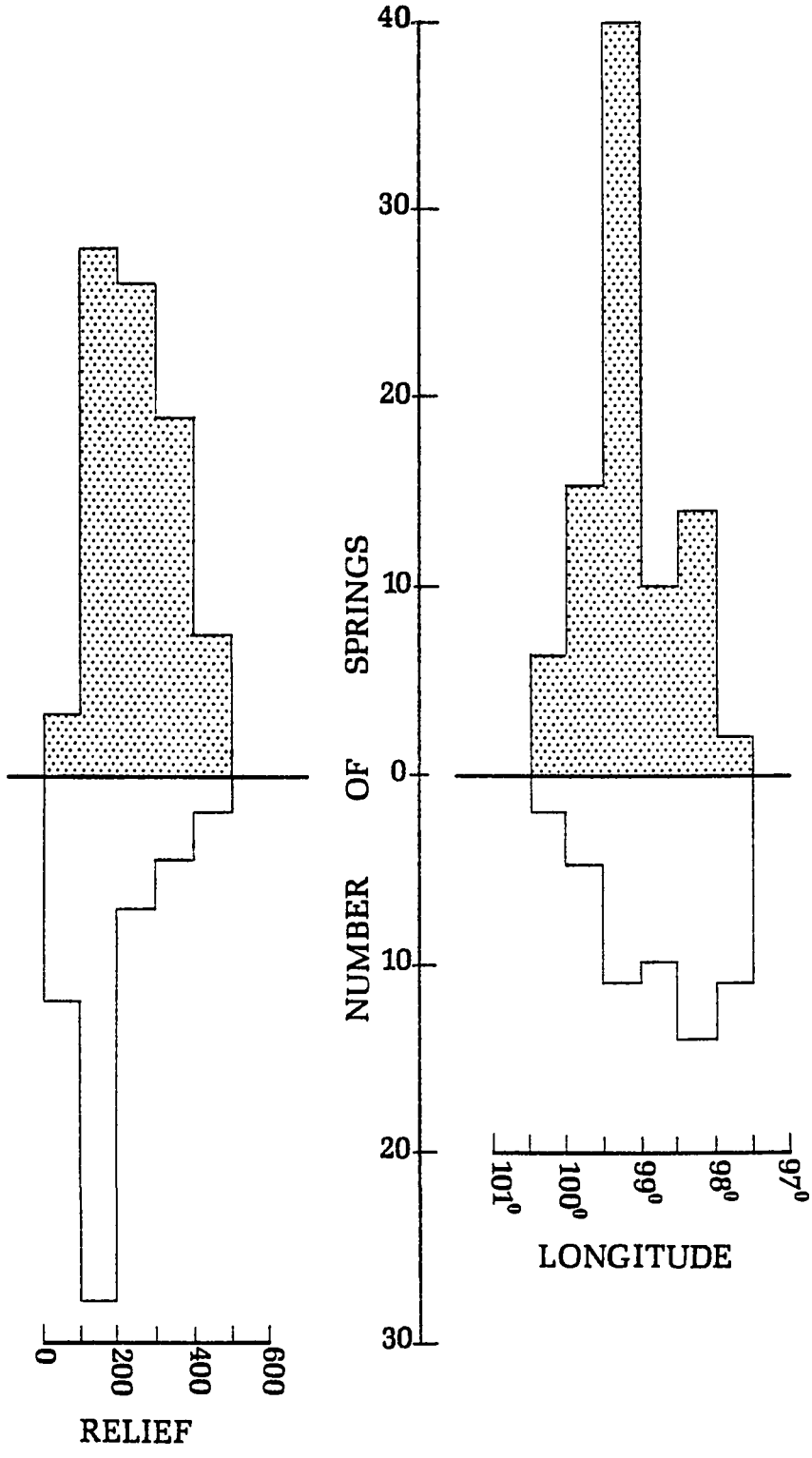

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ysis, as noted above; their inclusion reduces the level of significance separating the two distributions to 0.01. There is little if any predictive value in this result which is not due to the fact that the rivers on the eastern limb of the Plateau drain to the east. This results in a steady decrease in local topographic relief in passing from the Plateau surface eastward to the Balcones Fault Zone.

General Analysis of Distribution and Abundance

As is evident from Figure 12a, the proportion of inhabited springs increases in a regular relationship to increasing local topographic relief. This relationship is illustrated in Figure 13. The observed percent habitation values in Figure 13 can be generalized to yield a probability function, which can then be used to evaluate the likelihood that springs not examined in the field contain populations of *Eurycea neotenes*. This equation is:

$$P = 0.634(\log R)-0.531 \qquad (r = 0.93)$$

where P is the probability of habitation and R is local topographic relief in meters.

A survey of 468 7½' topographic maps covering the known distribution of the Texas *Eurycea* and surrounding areas shows a total of 1072 springs, 826 of which are located in the 127 7½' quadrangles which encompass the known distribution of the Texas *Eurycea*. The number of marked springs per quadran-

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Figure 13. The relationship between local topographic relief and the proportion of springs found to be inhabited by *Eurycea neotenes*. The heavy line is the probability function

$$P = 0.634(\log R) - 0.531 \qquad (r = 0.93)$$

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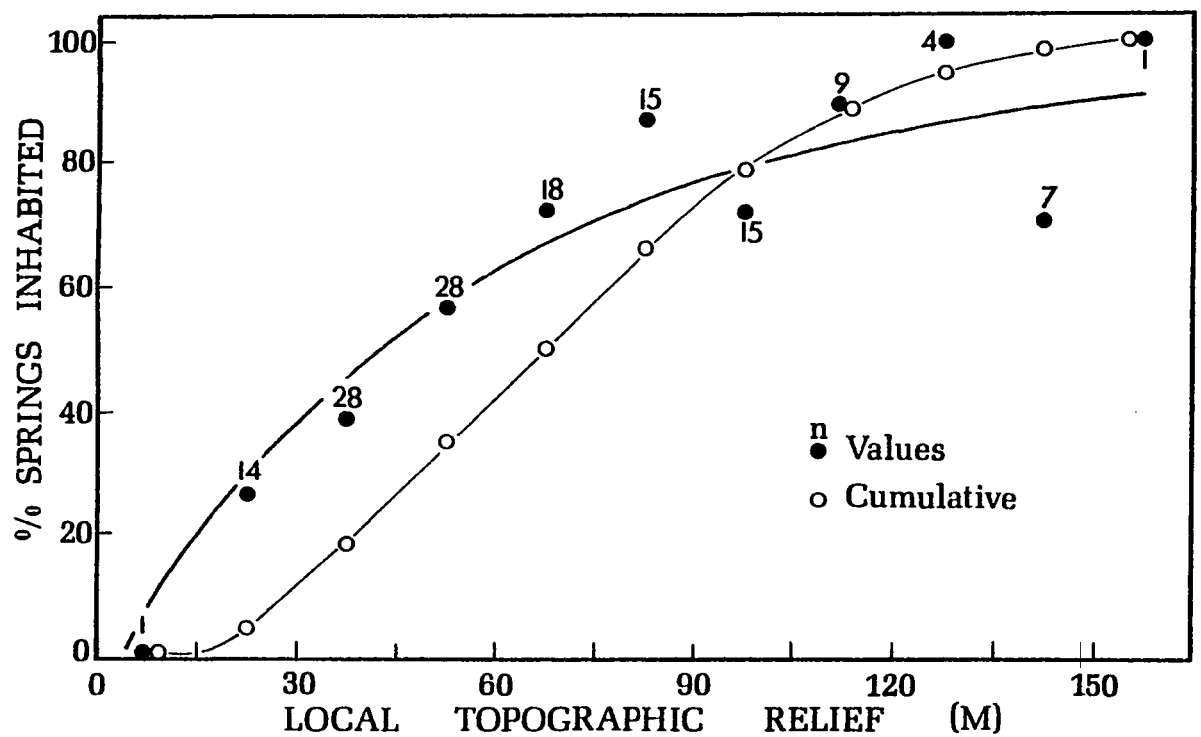

gle is indicated in Table 3 . Springs are about 10 times more numerous per unit area within the known range of the Texas Eurycea than in the adjacent peripheral zone. Further, springs within the known range have greater local topographic relief ($\bar{x}$ = 88.2 m) than do the peripheral springs ($\bar{x}$ = 49.5 m). The distributions of relief values transformed to probabilities of habitation are shown in Figure 14. Included in Figure 14 are the data for the 84 springs shown on topographic maps which were visited in the field (excluding seven fault zone springs, but including streamside resurgences). The two distributions are distinct: only 1.2% of the within-range springs have a less than 30% probability of habitation, compared to 13.8% of the peripheral springs; conversely, 52.5% of the within-range springs have a greater than 70% probability of habitation, contrasting with 9.3% of the peripheral springs. The mean probabilities of habitation for springs in each of the surveyed quadrangles are shown in Table 4 .

Insofar as the reasoning which links presence of salamanders with local topographic relief may be a valid abstraction of habitat requirements, the data in Figure 14 and Table 4 suggest that the great majority of populations of the Texas Eurycea occur within the presently known distributional limits as mapped in Figure 8. Springs in this region are far more numerous and likely to be considerably more reliable than springs in outlying areas. The three peripheral regions which show moderate to high probabilities of habitation are

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Figure 14. Frequency distribution of the probability of habitation (see text) for 1072 mapped springs within the polygon indicated on Figure 7. The 826 springs above the zero line on the figure are located in the 127 quadrangles encompassing the known range of *Eurycea neotenes*; the distribution of 246 mapped springs in 301 out-of-range quadrangles lies below the line.

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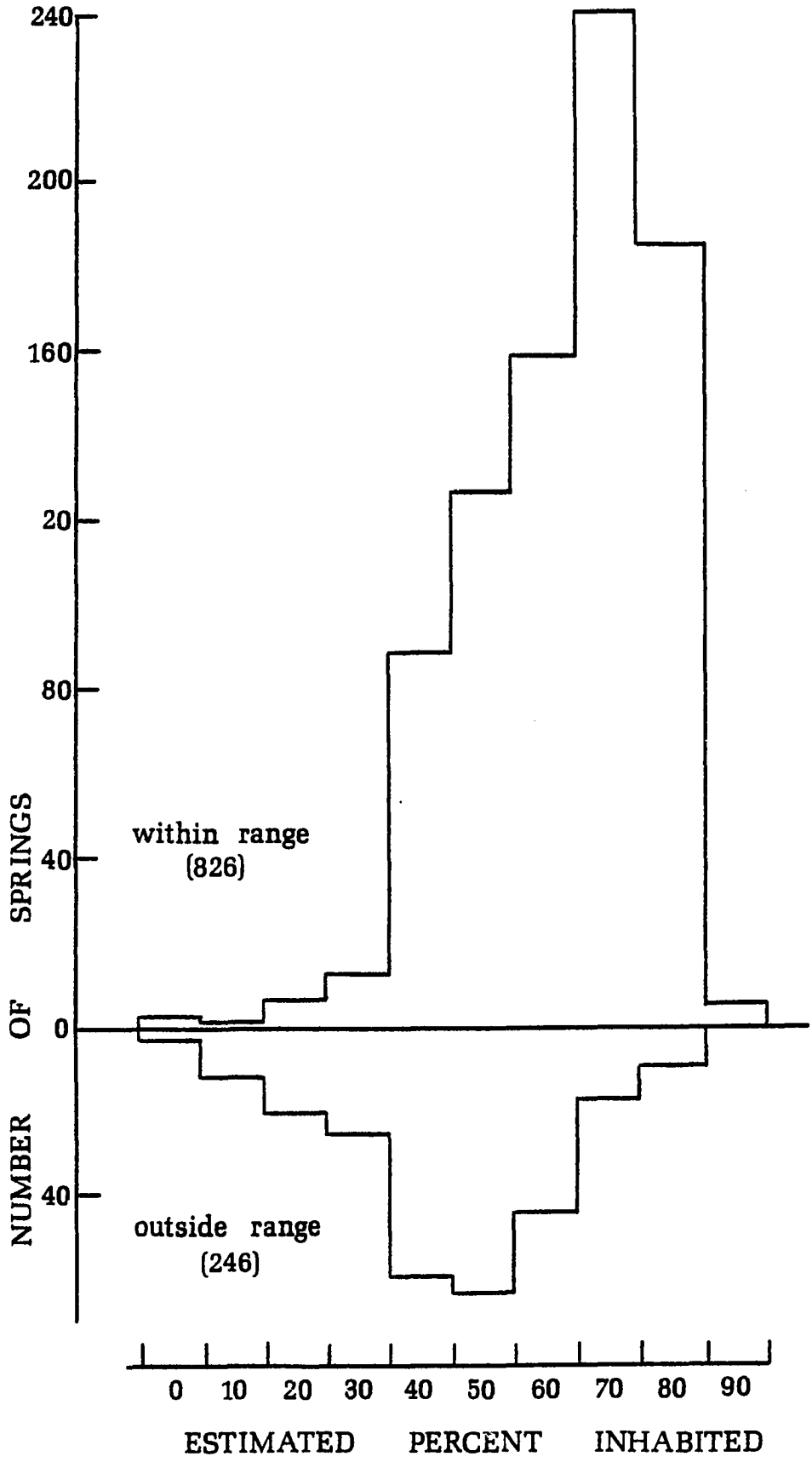

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Table 3. Numbers of marked springs on 468 7½' topographic maps enclosing the known distribution of the Texas *Eurycea*. The areal extent of the region surveyed is shown in Figure 7. Underlined entries indicate quadrangles wholly or partially within the known range of *Eurycea neotenes* (see Figure 8).

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	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
A																												0	5	0	0	0	0	2	0
B																										4	0	0	2	0	0	0	0	1	0
C																								2	0	15	0	6	1	0	0	0	0	0	0
D																						1	3	0	0	8	1	0	0	0	0	2	0	2	0
E																				2	1	1	0	0	0	0	7	0	0	1	1	2	0	0	1
F	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4	11	0	0	1	8	9	3	0	0	0	5	1	0	0	2	12	0	0	0	1
G	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	2	0	6	3	1	1	6	1	0	2	3	1	10	8	0	0	0	0
H	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	-	-	-	-	6	4	7	21	14	5	0	0	1	0	0	1	0	0	0	0
I	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	-	-	-	-	9	7	12	16	0	0	0	0	0	1	2	0	0	0	0	0
J	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2	3	1	3	0	0	0	0	6	6	2	2	1	0	0	0	0	0
K	1	0	0	0	0	3	0	0	0	0	0	0	8	0	0	0	1	21	13	4	23	26	10	6	2	0	8	5	5	0	0	0	0	0	0
L	0	0	0	0	0	1	0	0	0	2	1	1	7	31	13	7	0	9	14	8	0	3	0	2	2	3	2	0	0	0	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	1	0	1	34	43	12	4	4	25	12	5	1	12	3	3	6	2	1	2	0	0	0	0	0	0	0
N		0	1	0	0	0	0	0	0	0	2	1	10	33	9	43	8	14	37	14	10	8	15	11	0	11	0	0	0	0	0	0	0	0	0
O			0	0	0	0	0	0	0	0	0	5	12	15	9	2	14	3	15	3	9	0	8	3	0	0	0	0	0	0	0	1	0		
P				0	1	1	1	0	2	0	0	1	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0				
Q						3	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2						
R							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								

Table 4. Mean probabilities of habitation for springs mapped in the area shown in Figure 7; see text for methods of determination. Underlined entries indicate quadrangles wholly or partially within the known range of Eurycea neotenes (see Figure 8).

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	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
A																												0	37	0	0	0	0	31	0
B																										52	0	0	41	0	0	0	0	34	0
C																								35	0	58	0	37	37	0	0	0	0	0	0
D																						46	29	0	0	64	53	0	0	0	0	39	0	29	0
E																				56	43	58	0	0	0	0	65	0	0	37	29	44	0	0	18
F	0	0	0	0	0	0	0	0	0	0	0	0	0	51	48	51	0	0	67	43	29	37	0	0	0	75	62	0	0	34	53	0	0	0	11
G	0	0	0	0	0	0	0	0	0	0	0	51	53	0	0	0	0	29	0	59	53	51	58	64	62	0	34	67	67	61	48	0	0	0	0
H	0	0	0	0	0	0	0	0	0	0	0	0	59	-	0	-	-	-	-	53	54	48	59	78	62	0	0	37	0	0	37	0	0	0	0
I	0	0	0	0	0	0	0	0	0	0	0	0	0	64	-	-	-	-	-	53	53	46	48	0	0	0	0	0	18	41	0	0	0	0	0
J	0	0	0	0	0	0	0	0	0	0	0	0	68	57	0	0	0	51	54	46	54	0	0	0	0	58	56	47	53	59	0	0	0	0	0
K	81	0	0	0	0	71	0	0	0	0	0	0	73	0	0	0	59	61	58	61	64	53	48	56	53	0	46	53	48	0	0	0	0	0	0
L	0	0	0	0	0	84	0	0	0	58	65	84	82	72	70	65	0	62	62	63	0	66	0	61	53	53	48	0	0	0	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	72	0	81	78	75	83	72	72	66	81	78	48	56	58	61	53	53	65	65	0	0	0	0	0	0	0
N		0	48	0	0	0	0	0	0	0	73	62	68	83	79	81	82	80	77	74	56	67	72	70	0	68	0	0	0	0	0	0	0	0	0
O			0	0	0	0	0	0	0	0	0	70	62	78	75	61	73	86	86	77	72	0	67	64	0	0	0	0	0	0	0	29	0		
P				0	29	29	29	0	34	0	0	65	0	84	0	0	73	0	0	0	0	0	0	0	0	0	0	0	0	18	0				
Q						37	24	29	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14						
R							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								

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evaluated below.

Two general applications of the probability equation are possible within the scope of the assumptions made: (1) an estimation of the number of populations of Eurycea neotenes within the known range; and (2) an evaluation of the possibility that the actual range is more extensive than is presently known.

The first application involves an approximation derived from the products of the number of springs in each probability class of Figure 14 and the mean class probability of habitation. This process yields an estimate of 563 populations based on mapped springs alone. This must be regarded as a minimum figure, because not all springs are indicated on topographic maps (owing chiefly to reliance on aerial photomapping techniques). A partial correction can be made by use of the observation that 56 (40%) of the 140 springs located in the field on the Plateau proper were not shown on topographic maps; correction for this bias gives a modified estimate of 788 populations, which still must be regarded as a minimum estimate. This is because the correction factor is also biased because springs were initially sought by reference to maps, unmapped springs being discovered during field work or reported by local landowners. Correction for this source of error is difficult; one possible approach to determining its magnitude might be through the estimation of geologically probably spring sites where canyons intersect the Glen Rose-Edwards contact. The maximum error may

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be estimated by inspection of the two 7½' quadrangles containing the largest number of marked springs: these are the Jo Jan Van Camp and Rio Frio quadrangles (Real County), each with 43 mapped springs (Table 3). The estimation process uses admittedly subjective (but previously productive) criteria of elevation, proximity to continuous divide areas, aspects of canyon shape (narrowness, presence of sharp angular deflections in course, erosionally improbable bifurcations, etc.), and the presence of mapped "intermittent" streams (the mapping criteria for which appear to be the observation of isolated pools in aerial survey photographs; such pools are rare except in the vicinity of springs). This examination yields estimates of 83 and 99 probably unmapped spring sites in the Jo Jan Van Camp and Rio Frio quadrangles, respectively, suggesting that only about one third of the existing springs may be noted on topographic maps, rather than the figure of 60% derived from springs located in the field. From this it is probably valid to conclude that between 800 and 2400 epigean populations of *Eurycea neotenes* presently exist.

A comparably derived estimate (the sum of: number of springs/probability class, multiplied by the mean class probability) of the number of probable populations of *E. neotenes* peripheral to the known range indicates a figure of 169 populations when corrected for a 40% mapping bias. This estimate is probably incorrect for several reasons, the

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most basic being that the probability function indicates only the suitability of springs, actual habitation being dependent on the probability of colonization or recolonization in the past, and the likelihood of continously suitable habitat conditions existing since the time of distributional restriction to springs. Considerable distances of inhospitable habitat now separate most of the populations of E. neotenes, and it seems probable that most presently occupied springs have been continuously habitable since the time of distributional disjunction, as opposed to acceptance of a model in which recolonization of springs plays a major role. If the latter was a common phenomenon the distinction noted previously in terms of local relief and probability of habitation would not be expected, except under conditions of recolonization events involving short distances. The probability of recolonization is of course distance-dependent, and is thus more likely to be a factor in regions of high spring density than in areas where springs are few and widely dispersed. Some criterion of continuous suitability may provide a better estimate of the likelihood of the existence of distant peripheral populations than does reliance on a simple probability summation.

An arbitrary criterion of ≥ 70% probability of habitation (≥ 79 m local relief) may be selected as the limiting value for continuously habitable springs. Satisfying this criterion are 433 (52%) of the mapped springs within the known range, and 26 (10.6%) of the mapped springs peripheral to

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the known range. In terms of quadrangles, five of the 301 out-of-range units have mean probabilities of habitation ≥ 70%, compared to 34 such quadrangles within the known range (Table 4).

The 26 peripheral springs of ≥ 70% probability of habitation occur in three regions at varying distances from the known distributional limits of E. neotenes (distant west, peripheral north, and distant north). The likelihood of their containing populations of E. neotenes can thus be evaluated in terms of distance, as well as evaluations of hydrologic stability and the presence or absence of other adjacent springs with a ≥ 70% probability of habitation. These three regions are considered in turn below.

Three springs with high local topographic relief occur in isolation in major canyons in western and central Val Verde County, far to the northwest of known localities in the Nueces River drainage: one in the Pecos River canyon (Little Fiedeler Draw Quadrangle, 1K in Tables 3 and 4 , 122 m relief); and two along Dolan Creek, a major tributary of the Devils River (White Draw Quadrangle, 6K, 128 m relief, and Dry Devil NW Quadrangle, 6L, 134 m relief). Each of these sites appears to be hydrologically suitable, and may be found to be still inhabited by E. neotenes if the salamanders once occurred in the area, as is at least possible (see Chapter IV). These sites are indicated by open circles on Figure 8.

Sixteen springs with ≥ 70% probability of habitation are

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mapped along the Pedernales-Llano divide in northern Gillespie County, and others probably occur in the adjacent unmapped southern tributaries of the Llano River in southern Kimble County. Most of the springs in the Doss (20H, 1 spring, 91.5 m relief), Crabapple (23H, 1 spring 79 m relief), Willow City (24H, 11 springs, 79-156 m relief) and Blowout (25H, 1 spring, 79 m relief) quadrangles are developed near the base of the Edwards Group limestones adjacent to the margin of the Llano Uplift, and appear to be in hydrologically reliable situations. The remaining high-probability springs in this area occur in the Oxford Quadrangle (24G, 2 springs, 91.5, 152 m relief) of south central Llano County in Paleozoic limestones of the Llano Uplift. The hydrology of the limestones of the Llano Uplift is complex (Alexander and Patman, 1969; Mount, 1962; 1963); such information as is available suggests that the model of springs reliability employed herein is not valid in the Uplift itself. The small and disjunct areas of outcrop, and the complex patterns of faulting and folding characteristic of the limestones of the Llano Uplift (Barnes, _et al_., 1972) imply that springs here will be considerably less temporally reliable than are those on the Plateau proper. For these reasons populations of _E. neotenes_ appear to be unlikely to occur on the Llano Uplift.

Apart from the springs of the Oxford Quadrangle, those of the Pederales-Llano divide on the Plateau proper appear to have all of the requirements for habitation by populations of _Eurycea_. In addition to the 14 high-probability springs not-

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ed above an additional 59 springs are mapped in quadrangles 20I, 21I, and 20H-25H. This region of high spring density is contiguous with the known distribution of E. neotenes in Gillespie County (see Appendices I and II); thus it seems probable that populations of E. neotenes will be found to occur in the area indicated by a dashed line in Figure 8 . This prediction constitutes a test of the relief index as a measure of the probability of occurrence of populations of E. neotenes.

The springs of the third group of peripheral high-probability quadrangles are located along the canyon of the Colorado River in Llano, Burnet, San Saba and Lampasas counties, where the river transects the Llano Uplift. Springs in the Kingsland (26F, 3 springs, 98-101 m relief), Tow (26D, 2 springs, 79, 107 m relief) and Gorman Falls (26C, 2 springs, 79, 95 m relief) quadrangles satisfy the ≥ 70% criterion, but as is the case with the springs in the Oxford Quadrangle the probability model is likely to be invalid. Unlike the other high-probability springs on the Llano Uplift, this series along the Colorado River (including some or all of the 35 additional mapped springs) may be sufficiently temporally reliable to permit continuous habitation by populations of E. neotenes, for the reason that the floors of such large canyons generally reach the level of the local water table, and are thus highly reliable. The question thus becomes one of the probability that this region was once within the distribution of the Texas Eurycea. Only negative evidence is

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available which weakly suggests that populations of E. neotenes are unlikely to be found along the Colorado drainage on the Llano Uplift. This evidence consists of the observation that no populations are known along the Colorado drainage upstream from the Jollyville Plateau, and the observation that no troglobitic populations of Eurycea have been found in extensive surveys of the cave fauna of the region (Reddell, 1967; 1971).

Conclusion

Epigean populations of Eurycea neotenes are known to occur along the coastal margin of the Edwards Plateau from Williamson County south and west to Edwards County, with isolated populations in the Balcones Fault Zone in central Bell County and southeastern Val Verde County. Populations occur in all of the marginal drainages of the Plateau from the San Gabriel River south and west to the Nueces River, and extend inland to the headwaters of all streams south and west of the Blanco River. Populations are most numerous in the western portion of the range where geologic conditions are most suitable, becoming widely separated on the eastern limb of the Plateau. Populations in the Jollyville Plateau region are probably disjunct from the major portion of the range of E. neotenes. Populations are restricted in occurrence to the immediate vicinity of springs, and the probability of a given spring being inhabited by salamanders is related to a topographic index of spring reliability. Use of

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this index beyond the known distributional limits of E. neotenes suggests that the actual range is now essentially known, with the addition of a region in northern Gillespie County which shows a significant density of springs having high probabilities of habitation.

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CHAPTER IV

THE DISTRIBUTION AND DIVERSITY OF TROGLOBITIC POPULATIONS OF TEXAS *EURYCEA*

Introduction

As detailed in Chapter III, populations of *Eurycea neotenes* occur widely in reliable springs along the dissected coastal margin of the Edwards Plateau. These springs are the resurgence points of subterranean drainages, a small proportion of which have been found to be inhabited by populations of *Eurycea* as well. Many of these troglobitic populations are morphologically distinctive, and most appear to have been derived from epigean populations forced underground by the progressive, erosionally-mediated failure of springs. The mode of origin of troglobitic populations in the Texas *Eurycea* is tied to the origin of paedogenesis; for this reason a full discussion of the topic is deferred to Chapter V.

An important point to be kept in mind throughout this chapter is that very considerable distances separate most known troglobitic populations, and the caves they inhabit are usually small, local drainages which seem very unlikely on geologic and hydrologic bases to be linked to other caves in a more extensive network. At our present level of knowledge the most reasonable assumption seems to be that many troglobitic populations represent independent colonizations and an extensive occurrence of parallel adaptation. Certain systems of caves are known or strongly suspected to be continuous,as detailed below, but these represent a minority of

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cases. Aligned against this interpretation is the problem of ignorance of the actual number of troglobitic populations of Eurycea on the Edwards Plateau. In many areas, especially in the valleys of the larger streams and within the Balcones Fault Zone, cave systems are profusely developed and are actively consolidating into regional drainages. The overwhelming majority of these systems are inaccessible to collectors, but certainly accessible to Eurycea, and it is quite possible that only a small fraction of the total number of troglobitic populations are presently known or even have a reasonable probability of discovery. It may also follow that populations now thought to represent independent, isolated colonization events are linked by unknown populations.

Two types of evidence may be invoked against an extreme interpretation deriving from this uncertainty: first, despite extensive field work and communication with a diversity of experienced cavers, very few populations have been located in the course of this work whose existence was not known a number of years previously; and second, the morphological heterogeneity which exists among known populations, as documented below, suggests that if gene flow exists among many of these populations it must occur at a low level.

The purposes of the present chapter are four: first, to present the available distributional information concerning the occurrence of troglobitic populations; second, to briefly analyze the trends in character states seen among these populations; third, to attempt the recognition of adaptive

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grades of shared troglobitic adaptations within the set of populations; and fourth, to offer systematic interpretations from the viewpoint of the present anaylses which best fit the observed pattern of diversity.

Distribution of Troglobitic Populations

Twenty-eight troglobitic populations of Eurycea are presently known on the Edwards Plateau: these consist of 20 populations represented by specimens in available collections, two populations represented by specimens not available to me, five populations represented by sight records which I believe to be reliable, and one reported population of uncertain validity. The distribution of these populations on the Edwards Plateau is shown in Figure 15. The exact localities and locations of all specimens are presented in Appendix IV, and capsule descriptions of these sites and salamanders are provided below to the extent possible.

On a grand scale it is apparent that troglobitic populations occur widely across the Plateau, with two noticeably aggregated series of populations in Kendall and Comal Counties. The distribution of known populations is largely contained within the known range of epigean populations of Eurycea neotenes, with possible exceptions on the far western limit of the Plateau. In terms of geologic locations 18 of the troglobitic populations occur in caves developed in the Glen Rose Limestone of major stream valleys on the eastern limb of the Plateau, and 7 inhabited caves occur in the fractured Edwards Group or Devils River limestones of the

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Figure 15. The distribution of troglobitic populations of *Eurycea* on the Edwards Plateau. Counties are outlined, and the solid line marks the range of epigean populations of *Eurycea neotenes*. Filled circles represent populations for which specimens or sightings of known reliability exist. The open circle denotes a reported sighting. Localities marked are noted in Appendix IV.

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Balcones Fault Zone. Only three populations are known in caves of the Edwards Group and Devils River limestones of the Plateau inland from the Fault Zone; two of these (Sutherland Hollow Cave and Tucker Hollow Cave) are collapse structures along creeks; Haby Water Cave is the only major inhabited cave system of the Plateau surface.

Analysis on this scale is of limited utility; on the pages below the known cave localities and their populations of Eurycea are briefly described. This material is synthesized in the closing portion of this section, and combined with materials from Chapter II in the detailed analyses which comprise Chapters V and VI.

Descriptions of Caves and Troglobitic Populations

Capsule descriptions of the structure of each of the 28 caves known to be inhabited by populations of Eurycea are presented below, together with short characterizations of the populations therein. Caves are arranged in a east-to-west sequence within each county; where possible, reference is made to published descriptions of each cave (which are often rather superficial). Detailed descriptions and rough surveys of the caves visited in the course of this work are available in my field notes, together with surface maps of the locations of the caves; these notes are also referenced, and are on file in the Museum of Vertebrate Zoology.

The morphology of each of the troglobitic populations is treated in detail in later sections; the total number of available specimens, and short characterizations of each pop-

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ulation are presented here, followed by a brief, standardized description of coloration in life. More detailed color descriptions are contained in my notes, referenced above. The descriptions pertain to the majority of adult individuals; juveniles are usually darker, and more prominently patterned. Both the intensity and pattern of coloration varies widely among populations in life, and much of this distinctiveness disappears rapidly in preservative. This material is not intended to be analytical, since direct comparisons among populations in life were rarely possible under field conditions; it does illustrate an important way in which adjacent populations often differ strikingly. A few general observations on coloration are presented at the close of this section.

Unlike the epigean populations, the majority of troglobitic populations discussed here have been reported previously in checklists (Baker, 1961; Reddell, 1967b, 1971) as noted for each cave, and in most cases a few poorly preserved specimens had been accumulated by others prior to my work. The repositories of all specimens available from each cave are indicated in Appendix IV.

Bandera County

Sutherland Hollow Cave. This 20 m long shelter is a collapse structure developed in the middle Fort Terrett Formation in an undercut bank of a tributary of Jackson Hollow Creek; seepage from fractures in the back wall of the shelter forms a small pool which drains through breakdown into the adjacent

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creek. The cave is described in T.S.S. Bandera County files, and in my field notes (1974:124-126).

No specimens of Eurycea are available from this cave, though two series of E. neotenes were collected from epigean sites nearby. It is probable that salamanders inhabiting this cave are temporary immigrants from epigean populations. Eurycea were first reported from this locality in the T.S.S. files (undated).

Haby Water Cave. The entrance to this long cave is a collapse sink developed in the middle Segovia Formation of the Plateau surface, in a shallow internal basin between the headwaters of the Sabinal and Medina drainages. The cave leads southeast in a series of level, cobble-filled passages 3-5 m wide, separated by 3-10 m deep pits; several long, perched pools occur in the lower passages. It is penetrable for about 200 m before the passage becomes occluded with cobble and flooded. The discharge area for the system must lie 2-3 km away from the entrance, and over 100 m below. It is probable that no discrete spring outlet exists; its water may percolate into the basal burrowed member of the Fort Terrett Formation to emerge in numerous springs in both the Sabinal and Medina drainages. The cave is briefly described in T.S.S. Bandera County files, and in my field notes (1973: 244; 1974:119-124).

Two specimens of Eurycea have been collected in Haby Water Cave. They are stout, broad-snouted salamanders with relatively short limbs and large eyes (Table 8). Dorsal

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coloration in life is decidedly gray, the result of evenly and densely packed punctate melanophores on a light yellow base; reticulations or mottlings are absent. There are no pigment gaps nor iridophores associated with the lateral line organs. The lateral trunk is translucent, finely stippled with melanophores; iridophores are absent. A dark canthal line is prominent, and the postorbital bar is indistinct. The iris is pale gray.

Salamanders were first reported from Haby Water Cave by Reddell (1971).

Bell County

No troglobitic populations known.

Bexar County

Elm Springs Cave (Shavano Park Cave). This small deep cave is developed in the fractured Edwards Group limestones of the Balcones Fault Zone. A short passage leads to a 35 m pit, with an offset 20 m pit leading to a steeply sloping passage which reaches water level at a depth of about 80 m below the entrance. The flooded passage continues steeply downward. The cave is described in T.S.S. Bexar County files (see also my field notes 1976:6-7).

Eight specimens of *Eurycea* are available from Elm Springs Cave. This is an advanced troglobitic population, short-bodied with long limbs, large head and very reduced eyes (Table 7). The dorsal ground color in life is pale yellow, overlain with large, irregular blotches of expanded, purplish

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brown melanophores. Iridophores are scattered over the dorsal surface and surround the lateral line organs which are situated in irregular pigment gaps. The lateral body wall is translucent white, faintly reticulated with punctate melanophores; scattered iridophores are present. A faint dark canthal line is present and the postorbital bar is absent. The eyes are degenerate rounded aggregations of dark brown tissue buried beneath the skin.

This population was first reported by Sweet (1977b).

Blanco County

T Cave. This angular, joint-controlled cave is the former channel of a large spring developed in the basal upper Glen Rose Limestone on the floodplain of the Blanco River. It consists of a deep, narrow passage about 120 m in length, floored with large blocks of breakdown and a considerable depth of bat guano. Two small pools are located in an offset crawlway towards the rear of the cave. The cave is described in my field notes (1973: 225-227).

No specimens are available from T Cave; two individuals were seen but not collected. These are broad-headed, short-limbed salamanders with reduced eyes. The dorsal coloration is olive, overlain with dark longitudinal reticulations and mottlings, superficially resembling the pattern of local epigean populations of *E. neotenes*.

The T Cave population was first reported by Reddell (1971).

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Comal County

Fischer's Well. This is not a cave, but an old, 12 m deep well, constructed adjacent to a small spring emerging from the upper Glen Rose Limestone.

One specimen is available from this locality. It is a short-legged, small-headed salamander with large eyes (Table 8). On receipt after six years in preservative, the specimen was dull white, without any trace of pigmentation. No firm morphological evidence exists to indicate that this specimen represents a troglobitic population; rather, it seems to be an epigean individual bleached during storage.

This locality has not been previously reported.

Plumly Ranch Cave. This 2 m wide solution tunnel is developed at the base of the Glen Rose Formation and opens into the headwater canyon of Spring Branch (Creek). The passage extends for several dozen meters on a gravel and mud substrate; it is now dammed and backflooded. The cave discharges into Spring Branch through breakdown below the entrance. Plumly Ranch Cave is briefly described in Reddell (1964) and my field notes (1971:216-217; 1973:204-206).

Eurycea were first reported from this cave by Baker (1961). No specimens are now available; several individuals who have seen specimens recalled that they were brown in color.

Bender's Cave. This 2-3 m wide water cave is developed in the basal lower Glen Rose Limestone at the head of a tribu-

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tary canyon of Spring Branch. The passage is about 150 m long, bifurcating at two points into tributaries, each in excess of 100 m in length. Starting a few meters inside the entrance the cave contains 1-2 m of slowly flowing water on a clay and mud substrate. The cave discharges through breakdown a few meters below the entrance. The cave is described in Reddell (1964) and in my field notes (1971:218-22; 1973: 206-208; 213-215; 1974:112-116).

Eighty-eight specimens of Eurycea are available from Bender's Cave. These are large salamanders with long, relatively narrow heads, long limbs and reduced eyes (Table 7). The dorsal coloration in life is an even yellowish brown, with finely stippled melanophores on a pale yellow base. Lateral line pigment gaps are absent, but the lateral line organs are very conspicuously marked with iridophores. The lateral trunk is pale brownish gray, finely stippled with melanophores and moderately dense scattered iridophores. A dark canthal line is indistinct and a dark postorbital bar is present. The iris is pale yellow or gray.

This population was first reported by Reddell (1971).

Honey Creek Cave. This 300 m long solution tunnel is developed in the basal lower Glen Rose Formation, and opens as a spring on a tributary of the Guadalupe River. The passage is unbranched, 3-5 m wide, and contains 1-3 m of slowly flowing water on a clay and gravel substrate. The system extends southwest from the entrance towards a series of sinkholes about 1 km distant, and appears to drain a moderately large

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section of the first terrace of the Guadalupe valley. The cave is described in Reddell (1964), Mitchell and Reddell (1965) and in my field notes (1970:291-298; 1971:182-185; 1973:99-101, 178-181, 215-217; 1974:84-85).

Three morphologically distinct types of Eurycea have been collected in Honey Creek Cave and its adjacent spring flow. Six specimens are available of a small, short-limbed and small-headed Eurycea with large eyes (Table 7) which was referred to the "neotenes complex" by Mitchell and Reddell (1965, p. 25). The dorsal coloration in life is light olive, overlain by melanophores in a densely mottled pattern. Pigment gaps are small and iridophores adjacent to the lateral line organs are distinct. The lateral trunk is pale olive with faint dark reticulations. A dark canthal line and postorbital bar are present. The iris is silvery. Specimens were collected both in the cave and in the spring flow outside.

Four specimens of a second type are available; these are characterized by broader heads, more reduced eyes, and longer limbs than the first-mentioned specimens (see Figure 24 of Chapter VI). In life the dorsal coloration is pale yellow, overlain with blotches of faint (gray) melanophores, and finely stippled darker melanophores. Pigment gaps are absent in one specimen, large and irregular in the other three; in all, lateral line iridophores are prominent. The lateral trunk is white, lightly reticulated with punctate melanophores and a few scattered iridophores. A dark canthal line

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is present, and the postorbital bar is indistinct. The iris is dark gray or black. All four individuals were collected within the cave.

Sixty specimens of a third morphotype (named Eurycea tridentifera by Mitchell and Reddell, 1965) are available. These are short-bodied, large-headed and long-limbed salamanders with very reduced eyes (Table 7). The dorsal color in life is pale yellow, overlain by expanded (gray) melanophores arranged in large irregular patches. Pigment gaps are very irregular or absent, and the lateral line iridophores are well developed. The lateral trunk is translucent white, without melanophores. A faint dark canthal line is present, and the postorbital bar is absent. The tiny eyes are dark and frequently irregular in outline.

Eurycea were first reported from Honey Creek Cave anonymously (1959); see also Mitchell and Reddell (1965).

Kappelman Salamander Cave. This small sinkhole is developed in the lower Glen Rose Formation of the Cibolo Sinkhole Plain. A small depression leads to a 4 m deep pit opening into a low room, from which a very narrow crevice leads down 15 m to a horizontal passage 0.5 m in diameter which is filled with water on a cobble substrate. The cave is briefly described by Reddell (1964) and in my field notes (1973: 172-176; see also 1975:104-106).

Five specimens of Eurycea are available from Kappelman Salamander Cave. They are slender, short-bodied salamanders with large, broad heads, long limbs, and very reduced eyes

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Table 7). The dorsal coloration in life is pale cream, overlain with finely stippled melanophores in a faint pattern of longitudinal reticulations. Pigment gaps are irregular, and lateral line iridophores are prominent. The lateral trunk is translucent white without melanophores or iridophores. A very faint canthal line is present, and a postorbital bar is absent. The eyes are rounded, dark brown masses of tissue buried beneath the skin.

This population was first reported by Reddell (1971).

Calmbach Cave. This cave is a sinkhole developed in the lower Glen Rose Limestone of the Cibolo Sinkhole Plain. Its precise location and structure are not known.

A single specimen of Eurycea is available from Calmbach Cave. It is a short-bodied, large-headed salamander with long limbs and very reduced eyes. In preservative the dorsal coloration is white, overlain with faint longitudinal reticulations of melanophores. Lateral line gaps are irregular; the presence of iridophores cannot be determined. The lateral trunk is white, without melanophores. A faint canthal line is present, and a postorbital bar is very faintly indicated. The eyes are rounded, dark, and buried beneath the skin (see Table 8).

This population was first reported by Sweet (1977b).

Grosser's Sinkhole. This small but long cave is developed in the lower Glen Rose Limestone of the Cibolo Sinkhole Plain. The entrance is a 15 m pit, which opens into a 1-2 m

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wide gently sloping, joint-controlled passage trending east-northeast for about 180 m to a second 10 m pit, which has not been entered. The passage contains several long, shallow pools on a substrate of clayey mud; water drains between pools and over the second pit in a muddy rivulet. The cave is briefly described by Reddell (1964) and described in detail and mapped in my notes (1970:280-289; 1973:223-225; 1974:62-65, 171-172).

Twenty-two specimens are available from Grosser's Sinkhole. They are slender, short-bodied salamanders with large broad head, long limbs and very reduced eyes (Table 7). The dorsal coloration in life is pale cream to white, overlain with punctate and diffuse melanophores in a longitudinally reticulated or faintly mottled pattern. The skin imparts a purple gloss dorsally. Pigment gaps are irregularly present, or absent, and lateral line iridophore deposits are present in a few specimens but generally lacking. The lateral trunk is translucent white, without melanophores or iridophores. A faint dark canthal line is present, and a postorbital bar is faintly present in a few individuals. The eyes are tiny, round and dark brown, buried in the tissues of the snout.

Eurycea were first reported from Grosser's Sinkhole by Reddell (1971).

Badweather Pit. This small sinkhole is developed in the lower Glen Rose Limestone of the Cibolo Sinkhole Plain. The entrance is a 10 m sinkhole, with a crevice at the bottom

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leading to a 40 m long, gradually stepped, joint-controlled passage 1-3 m wide containing 0.5-1 m deep pools of standing water on a mud and cobble substrate. The accessible passage breaks into five water-filled crawls about 25 m below the entrance elevation. Badweather Pit is briefly described by Reddell (1964) and described in detail and mapped in my field notes (1974:62, 103-106, 170-172, 186-188).

Forty-seven specimens of Eurycea are available from Badweather Pit. They are large, short-bodied salamanders with large, broad heads, long limbs, and very reduced eyes (Table 7). The dorsal coloration in life is pale pink, blotched or finely mottled with irregular gray melanophores. The skin imparts a dull purple gloss to the dorsum. Pigment gaps are irregular or absent, and lateral line iridophores are few and indistinct. The lateral body wall is translucent pink, with a few iridophores but without melanophores. A faint dusky canthal line is present, and the postorbital bar is absent. The eyes are tiny, regular in form and black, buried in tissue.

Eurycea were first reported from Badweather Pit by Reddell (1971).

Edwards County

No troglobitic populations known.

Gillespie County

No troglobitic populations known.

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Hays County

No troglobitic populations known.

Kendall County

Kneedeep Water Cave. This small, horizontal cave is developed in the lower Glen Rose Limestone on a short tributary of the Guadalupe River. Like other caves in the region it is based at the contact of the Glen Rose Formation and the Hensel Sand, and contains a long pool of standing water on a substrate of mud. No other descriptions of this cave are available.

No specimens of Eurycea have been collected in this cave. According to William H. Russell (personal communication, 1978), they are light brown in color.

This population has not been reported previously.

Little Water Cave. This cave is a small passage developed at the Glen Rose-Hensel contact at the head of a short tributary of the Guadalupe River. It contains a long pool of slowly flowing water, which discharges through breakdown below the entrance. The cave terminates in a shallow sinkhole on the first terrace of the Guadalupe valley. The cave is described in T.S.S. Kendall County files, and in my field notes (1973:218-220).

No specimens of Eurycea have been collected in Little Water Cave. According to William H. Russell (personal communication, 1973, 1974), these are small, brown salamanders with relatively short limbs and moderately reduced eyes.

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This population was first reported by Reddell (1967b)

Deadman's Cave (Century Caverns, Cave-Without-A-Name). This large solution tunnel is the outlet of a regional subterranean drainage; the alternate names listed above are applied to a sinkhole entrance to the upper levels of the system, which drains an area of several hundred hectares on the floodplain of the Guadalupe River. Passages are developed in the lower Glen Rose Limestone, and reach base level on the upper surface of the Hensel Formation. The outlet lies at the base of a cliff cut by Spring Creek; it consists of a branching horizontal passage 6-8 m wide and several hundred m long, which communicates with the upper levels by a series of pits and narrow, stepped passages. The system has over 4 km of mapped passage (Pate, 1978). The lower passages contain 1-2 m of standing water on a substrate of mud and clay. The cave is described in unpublished materials in the T.S.S. Kendall County files, and in my field notes (1974:148-152).

Fifteen specimens of Eurycea are available from Deadman's Cave. These are rather short-legged, broad-snouted salamanders with moderately reduced eyes (Table 7). The dorsal coloration in life is generally brown (tinged with orange fat deposits), with fine mottlings and reticulations of melanin on a pale yellow base; one adult in the series was cream with gray mottling. Lateral line pigment gaps are small, with distinct concentrations of iridophores marking the lateral line organs. The lateral trunk is tan, reticulated with faint melanophores and numerous scattered irodophores. A

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dark canthal line is present, and the postorbital bar is indistinct. The iris is dark gray.

Alzafar Water Cave (Camp Alzafar Cave). This long, joint-controlled solution tunnel is developed at the Glen Rose-Hensel contact on a short tributary of the Guadalupe River. About 1 km of this 1-3 m wide cave has been mapped; it leads southwest from the entrance toward a group of sinkholes on the first terrace of the Guadalupe valley. The cave contains 0.5-1 m of standing water on a gravel and clay substrate. The system flowed as a spring as recently as 1925, but now flows only after heavy rains. The cave is described in T.S.S. Kendall County files, and in my field notes (1973: 219-221; 1974:66-69).

Fourteen specimens of Eurycea are available from Alzafar Water Cave. They are large, moderately long-legged salamanders with narrow snouts and reduced eyes (Table 7). The dorsal coloration in life is a dusky yellowish brown, with punctate melanophores in fine reticulations on a pale yellow base. Pigment gaps are small or absent, and the lateral line iridophores are prominent. The lateral trunk is gray, with evenly spaced punctate melanophores on a translucent white base; lateral iridophores are absent. A dark canthal line is present, and a postorbital bar is lacking. The iris is dark gray.

This population was first reported by Reddell (1967b).

Golden Fawn Cave (Golden Fawn Dude Ranch Water Cave). This

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small water cave is developed at the Glen Rose-Hensel contact near the head of a small tributary canyon of the Guadalupe River. The cave is a 1 m diameter passage leading southwest at least 15 m (reportedly in excess of 800 m), and is nearly filled with standing water on a cobble substrate. Water level in the cave is about 2 m below the adjacent canyon bed. It is likely the passage originates in a group of sinkholes on the first terrace of the Guadalupe valley, about 600 m to the southwest of the entrance. The cave is described in my field notes (1971:185-187; 1974:88-90).

One specimen is available from Golden Fawn Cave. It resembles salamanders from Alzafar Water Cave, 1.4 km to the east, in all respects except in lacking lateral line iridophores (see Table 8).

This locality was first reported by Reddell (1967b).

Victor Phillip Water Cave. This small flowing water cave is developed at the Glen Rose-Hensel contact in a tributary canyon of the Guadalupe River, 1.1 km west-southwest of Golden Fawn Cave. It consists of a low, 1 m wide passage with up to 0.5 m of slowly flowing water on a sandy substrate; it is penetrable for about 20 m before the passage is filled by the stream. Like other caves in the area the passage trends southwest. The cave is described in my field notes (1974: 144-148).

Twenty-one specimens of *Eurycea* are available from this site; all were collected in the stream outside of the cave, though they resemble a single individual seen within. They

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are small, short-legged salamanders with narrow heads and large eyes (Table 7). The dorsal coloration in life is dark olive brown, produced by the concentration of melanophores on a light yellow base, with indistinct darker mottling. Pigment gaps are small and regular, and the lateral line iridophores are indistinct. The lateral trunk is gray, with finely stippled melanophores and without iridophores. A dark canthal line and distinct postorbital bar are present. The iris is dark gray.

This population was first reported by Reddell (1967b).

Behr's Cave. The entrance to this small cave is a sinkhole developed in the top of the lower Glen Rose Limestone on a broad terrace above the valley of the Guadalupe River. A series of offset pits drops about 15 m to a siphon communicating with a narrow, muddy horizontal passage containing isolated pools. Behr's Cave is apparently a terminal tributary of an unmapped regional system draining a small section of the Guadalupe floodplain. The cave is described in my field notes (1974:99-103).

Four specimens of Eurycea are available from Behr's Cave. They are large-headed, relatively long-limbed salamanders with large eyes (Table 7). The dorsal coloration in life is a medium brown, produced by fine, densely-packed melanophores overlying a light brown ground color; concentrations of melanophores in the dorsal myoseptal grooves are noticeable as faint dark chevrons. Indistinct iridophores mark the lateral line organs, which are not enclosed in pigment gaps. The

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lateral trunk is translucent white, evenly stippled with melanophores. A dark canthal line is present, and the postorbital bar is absent. The iris is pale gray.

This population has not been reported previously.

Cascade Caverns and Cascade Sinkhole. This cave system opens in two 20 m deep sinkholes developed in the lower Glen Rose Limestone of the Cibolo Sinkhole Plain. Cascade Caverns is a commercially-developed cave with several hundred meters of 4-8 m wide passages; the lower passages contain a series of shallow pools, which are now heavily modified. Cascade Sinkhole is located about 600 m west-southwest of Cascade Caverns; a short, water-filled passage intersects a long, 2-3 m wide fissure containing 0.5-1.5 m of standing water which extends for about 700 m east-northeast. The passages of Cascade Caverns and Cascade Sinkhole nearly communicate at several points, and the two caves are here considered part of a single system. The caves are described in T.S.S. Kendall County files, and in my field notes (1970:247-249, 298-300; see also 1976:4-5).

Twenty-two specimens are available from the Cascade system (14 from Cascade Caverns, and eight from Cascade Sinkhole). These are large, slender salamanders with broad heads, rather short limbs, and moderately reduced eyes. The dorsal coloration in life is tan, with finely stippled melanophores tending to form a pattern of small, longitudinal reticulations. Pigment gaps are small but regular, and the lateral line iridophore deposits are distinct but small. The later-

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al trunk is translucent white, densely stippled with punctate melanophores; a few scattered iridophores are also present. A dark canthal line is present, and the postorbital bar is present, either prominent or indistinct. The iris is dark in most specimens, though occasionally golden (see Table 7).

This population was apparently first reported by Wright and Wright (1938), though Uhlenhuth's hearsay record (1921) for Typhlomolge rathbuni ("Burnet Cave, near Burnet") may apply to this site, which was sometimes called Boerne Cave in the past. The names Burnet and Boerne are pronounced in a similar fashion locally. This population was named Eurycea latitans by Smith and Potter (1946).

Schwarz Cave. This sinkhole is developed in the lower Glen Rose Limestone on a tributary of Balcones Creek, at the extreme western edge of the Cibolo Sinkhole Plain. According to James R. Reddell (personal communication, 1974), a water passage leads away from the base of the entrance pit for a considerable distance.

No specimens of Eurycea are available from Schwarz Cave. According to Reddell the salamanders resemble those of the Cascade system.

This population has not been previously reported.

Kerr County

No troglobitic populations known.

Kinney County

No troglobitic populations known.

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Medina County

Valdina Farms Sinkhole. This large cave opens in a sinkhole in the Edwards Group Limestones of the Balcones Fault Zone. A 30 m deep pit leads to an offset 20 m pit, which opens into a gently, sloping passage, 3-4 m wide, extending east-northeast and west-southwest from the pit. About 400 m of passage is penetrable, lying mostly west of the entrance. On the east the passage siphons in a muddy pool; lower sections of the western passage hold long, 1-2 m deep pools of clear water on a mud substrate. These pools are linked by a rapid, gravel-bottomed stream whose course is chiefly beneath the breakdown deposits which separate the pools. The cave is described and mapped in Reddell (1967a) and in my field notes (1973:162-165; 230-234; 1974:128-133).

Forty-two specimens of Eurycea are available from Valdina Farms Sinkhole. Individuals are very variable in both proportions and coloration; some individuals closely resemble epigean specimens of E. neotenes in proportions, while others are broad-headed and long-limbed, with large to very reduced eyes. Coloration also varies markedly; individuals resembling E. neotenes in proportions are generally yellowish brown, reticulated with melanophores dorsally. Pigment gaps are absent, and lateral line iridophores are distinct. The lateral trunk is gray, finely stippled with melanophores. A distinct canthal line and postorbital bar are present. The iris is silvery or dark gray. Other individuals are pale yellow dorsally with an evenly reticulated pattern of punc-

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tate melanophores, or with irregular purplish brown patches of expanded melanophores, or with irregular, very faint gray patches of expanded melanophores. The pigment gaps are irregular or absent, and lateral line iridophores are indistinct. The lateral trunk is pinkish, with stippled melanophores. A faint canthal line is present, and the postorbital bar is absent. The iris may be silvery or dark gray. These individuals do not display consistency in body proportions; limbs may be long or short, eyes large or reduced, head broad or narrow in a seemingly independent fashion.

This population was first reported by Baker (1957), who described it as a new species, Eurycea troglodytes. The unusual attributes of this population are considered further in Chapter VI.

Real County

Tucker Hollow Cave. This cave is a 20 m long collapse chamber in the Devils River Formation at the head of a small canyon; it is floored with large slabs of breakdown, and has two small rimstone pools aligned along the rear wall. Water seeps into these pools from joints in the wall, and the overflow percolates through the breakdown to emerge in a feeble spring in the canyon about 15 m below. The cave is described in T.S.S. Real County files, and in my field notes (1974:78-80, 161-162).

Ten specimens are available from Tucker Hollow Cave. They are stout-bodied, short-legged salamanders with large, broad heads and slightly reduced eyes (Table 7). In life

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they are a pinkish tan, heavily streaked and mottled with melanophores and scattered iridophores dorsally. Lateral line pigment gaps are small, and iridophores surrounding the lateral line organs are indistinct. The lateral trunk is pale pink with densely stippled melanophores and scattered iridophores. A dark canthal line is present, and the post-orbital bar is absent. The iris is light gray.

This population was first reported by Reddell (1971).

Travis County

Barton Springs. This site is not a cave; rather, it is a complex of springs issuing from the Barton Springs Fault, a local component of the Balcones Fault Zone developed in Edwards Group Limestones. Associated with these springs is a large subterranean system which is probably very similar to Airman's Cave (Russell, 1975). The latter cave represents an old outlet of the aquifer now discharging through Barton Springs and consists of a series of narrow, angular, joint-controlled passages; 3.4 km have been mapped, and the system is certainly much longer. The spring is described in my field notes (1970:208, 305; 1971: 165; 1973:138; 1974:53; see also 1976:2-3, 1978:100).

Forty-seven specimens of Eurycea are available from Barton Springs. Unlike other Fault Zone spring populations (see Chapter III), these salamanders are troglobites; individuals discharged from the spring exits can be found beneath stones and debris in the spring basin (now modified as a wading pool). These are slender, long-limbed salamanders with rela-

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tively small, narrow heads and reduced eyes (Table 7). The dorsal coloration in life is rather variable, owing to differing amounts of melanophores and iridophores among individuals; the dorsum may be yellowish brown, pale purplish brown, or pale purplish gray. The base color dorsally is pale yellow, overlain by expanded melanophores aggregated into irregular patches which may cover from all to about a third of the dorsum. Iridophores are generally present dorsally, and in some individuals are so dense as to obscure the melanophore patches. Small pigment gaps are present, and the lateral line organs are marked by iridophores. The lateral trunk is translucent white with fine melanophore stippling and abundant iridophores. A dark canthal line is present, and a dark postorbital bar is present but indistinct. The iris is golden.

This population was first reported by Baker (1961).

Salamander Cave. This very small cave is developed in the Edwards Group Limestones of the Balcones Fault Zone. A narrow crevice drops about 5 m into a short, joint-controlled passage which intersects a small stream flowing at right angles to the passage. The cave is described in Reddell and Russell (1961) (see also my field notes, 1973:138, 217-218; 1974:135).

Nine specimens of *Eurycea* are available from Salamander Cave. They are robust, large-headed salamanders with relatively short limbs. No living individuals have been available; preserved specimens are light brown dorsally with even-

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ly stippled melanophores and a few darker longitudinal mottlings. Pigment gaps are absent. The lateral trunk is finely stippled with melanophores, and shows indications of scattered iridophores. A dark canthal line is prominent and the postorbital bar is indistinct. The iris color in life is not known (see Table 7).

This population was first reported by Reddell (1967b).

Uvalde County

Cave near Concan. A fully metamorphosed specimen of Eurycea was reportedly found in an unlocated cave a short distance northeast of Concan (B.C. Brown, personal communication, 1970; Sweet, 1977a). No further information on this site or specimen is available.

Carson Cave (Whitecotton Well). The entrance to this cave is a senile spring exit developed in the basal Devils River Limestone on the east slope of Long John Draw, a tributary of the Nueces River. A long, low passage extends northeast from the entrance, with a shallow pit near the entrance leading to the present water level in a low passage leading south-southwest. The stream passage is 1-1.5 m wide, and penetrable for about 20 m; the stream flows south-southwest in shallow pools and riffles on a gravel substrate. The cave is described in my field notes (1973:235-239; 1974:81-82, 155-158).

Fifteen specimens of Eurycea are available from Carson Cave. These are stocky salamanders with moderately long

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limbs, small heads, and reduced eyes (Table 7). Dorsal coloration in life is tan, overlain with melanophores arranged in longitudinal reticulations and streaks; pigment gaps and iridophores associated with the lateral line organs are reduced or absent. The lateral body wall is faintly stippled with melanophores, and lacks iridophore deposits. A dark canthal line is prominent, and the postorbital bar is indistinct. The iris is silvery.

Eurycea were first reported from Carson Cave by Reddell (1967b) and Bogart (1967).

Val Verde County

Fourmile Cave (Sally Cave). Two shallow collapse sinks lead into this labyrinthine cave developed in the lower Devils River Limestone. Short passages and pits are developed along joints in a seemingly random fashion both laterally and vertically throughout an area of a hectare or more; the lack of established channels indicates a long history of slow flow rates, and that accessible parts of the cave are far removed from a discharge point. The system is probably a tributary of San Felipe Springs, located about 8 km southeast. Numerous shallow pits and inclined passages lead to muddy pools of standing water, which appear to be linked by flooded passages. Parts of the cave are mapped and described in Reddell (1963), and in my field notes (1973: 228-230; 1974:174-178, 186-187).

Nine specimens of Eurycea are available from Fourmile Cave. They are very slender salamanders, with moderately

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long limbs, broad snouts, reduced eyes, and elongate gill rami (Table 7). The dorsal coloration in life is a plain purplish gray, the result of finely stippled melanophores on a tan to cream base color, with a dull purple sheen imparted by the skin. The lateral line organs are not marked by pigment gaps or distinct iridophores deposits. The lateral body wall is transparent or finely stippled with melanophores, and lacks iridophores. A dark canthal line is present, and the postorbital bar is absent. The iris is dark brown.

Eurycea were first reported from Fourmile Cave by Baker (1961); a specimen from this population was figured by Bogart (1967, Plate 5d).

Comstock Crack. This deep fissure is developed in the uppermost Devils River Limestone along Cow Creek, a tributary of the Rio Grande. The cave is an enlarged joint which takes water when the creek flows; a 20 m long sloping entrance passage meets an offset pit which drops about 45 m to a sandy slope at water level, below which the pit continues. The cave is described in my field notes (1974:172-175, 183-185).

No specimens of Eurycea are available from Comstock Crack. The cave is provisionally included in this listing on the basis of two old, apparently independent reports (of unknown reliability) of salamanders having been observed in a deep cave along Cow Creek. Of eight caves located in the immediate vicinity, Comstock Crack is the only one which can be followed to water; this point and particulars of the descriptions of the salamander-containing cave indicate that

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the reports apply to this pit.

Williamson County

No troglobitic populations known.

From the descriptions of cave systems presented above and the general discussion of the erosional history of the Plateau presented in Chapter II, it seems reasonable to conclude that many of the inhabited caves other than those of the middle Guadalupe valley and the Cibolo Sinkhole Plain are mutually isolated. Most of these systems are developed in the fractured strata of the inland margin of the Balcones Fault Zone. Of these, Salamander Cave, Barton Springs, Elm Springs Cave, Fourmile Cave and perhaps Comstock Crack are all closely associated with the main subdivisions of the Fault Zone Aquifer; Sutherland Hollow Cave, Haby Water Cave, Tucker Hollow Cave, and Carson Cave all appear to discharge into surface drainages inland from the aquifer, and thus are not linked to it by subterranean channels. The latter series of caves are indisputably isolated from one another; in the former series direct subterranean connections probably exist among the caves, which are mutually separated in all but one case by distances in excess of 40 km. Salamander Cave and Barton Springs are only 12 km apart, but are separated by the canyon of the Colorado River, which transects and isolates the Fault Zone Aquifer between the two sites (Chapter II).

The caves of the middle Guadalupe valley are closely

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spaced, and thus may have a greater possibility of being interconnected. The degree of isolation likely to exist among them is discussed in detail in Chapter VI, and has been treated in a general fashion in Chapter II; the available evidence indicates that most are mutually isolated local systems. Alzafar Water Cave, Golden Fawn Cave and possibly Victor Phillip Water Cave have the greatest likelihood of being parts of a single system.

All of the caves of the Cibolo Sinkhole Plain are very probably tributaries of a single diffuse drainage system, which is linked to the Fault Zone Aquifer through the extensive cave systems of northern Bexar County (Chapter II; see also Chapter VI). The accessible portions of these caves lie well above the level of major passages linking them, but their behavior as a hydrologic unit during floods demonstrates the existence of such large, interconnecting channels. On this basis the four populations of advanced troglobitic Eurycea known from the Cibolo Sinkhole Plain (Kappelman Salamander Cave, Calmbach Cave, Grosser's Sinkhole and Badweather Pit) are not felt to be isolated from one another; further, they are unlikely to be strongly isolated from the similar population in Elm Springs Cave to the south. The advanced troglobitic population inhabiting Honey Creek Cave in the Guadalupe valley strongly resembles the populations of the Cibolo Sinkhole Plain, and probably represents an outlier of the group. The affinities of the Honey Creek Cave population are documented below, and considered in de-

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tail in Chapter VI. Also present on the Cibolo Sinkhole Plain are one or possibly two populations of a less advanced troglobitic salamander (Cascade Caverns System, ? Schwarz Cave). The problems involved in the occurence of two types of troglobitic populations in the interconnected cave systems of the Cibolo Sinkhole Plain are noted in Chapter VI.

Trends in Coloration

Several generalizations may be made concerning trends in coloration among troglobitic populations. This initially requires a general description of the coloration of epigean specimens of Eurycea. Most epigean populations of Eurycea are yellowish olive to brownish olive dorsally, with prominent darker mottling or longitudinal reticulations. Pigment gaps and lateral line iridophores are of variable occurrence, but both are present in a majority of populations. The lateral trunk of epigean Eurycea is generally pale, with faint longitudinal reticulations of melanophores; lateral iridophore deposits are very seldom noted. Dark canthal lines and dark postorbital bars are prominent in most epigean populations. Iris color varies from silvery through gold to dark gray or brown.

Troglobitic Eurycea may be light brown, tan, pale yellow or nearly white dorsally, but virtually never show an olive tone (the salamanders in T Cave may be an exception). Brown populations (Guadalupe valley caves) usually lack strong dark reticulations or mottling on the dorsum, and pig-

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ment gaps are usually indistinct; lateral line iridophores may be prominent or indistinct. Populations with a generally tan dorsal coloration usually also show dark reticulations or mottling, and tend to have distinct pigment gaps and prominent lateral line iridophores. In both brown and tan populations the lateral trunk tends to be finely stippled with melanophores; scattered lateral iridophores are usually present in tan populations only. Populations of a paler dorsal color (cream or pale yellow) generally have expanded melanophores grouped into irregular blotches and longitudinal streaks, with pigment gaps poorly developed or absent; the skin often shows a dull purple gloss. Lateral line and lateral trunk iridophores are often prominent; the lateral trunk tends to lack melanophores. A dark canthal line is present in all populations, tending to become fainter as the dorsal coloration becomes more pale; the postorbital bar characteristic of epigean Eurycea generally persists in brown and tan populations (though it is often faint), and is usually absent in the most depigmented populations. Iris color shows no clear trend among brown and tan populations; eye degeneration has proceeded to the point that the iris is lacking as a structure in the most depigmented populations.

The majority of troglobitic populations of Eurycea fall into these general characterizations (brown without darker dorsal markings, tan with darker dorsal streaks or mottling, and pale yellow with irregular gray or purplish brown patches). Four populations show significant divergences from

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this trend: the Barton Springs salamanders are unique in displaying a heavy concentration of iridophores on the dorsum; the Haby Water Cave salamanders are gray; the Tucker Hollow Cave salamanders are pinkish; and salamanders from the Fourmile Cave population are dull purplish gray dorsally.

Trends in Proportional and Meristic Characters

There exists considerable morphological diversity among troglobitic populations of the Texas Eurycea. Taken as a whole, these salamanders display varying degrees of troglobitic adaptation in characters such as: intensity of pigmentation (as discussed above); numbers of trunk vertebrae and teeth; relative eye and head size; and relative limb length. All of these features show trends in the troglobitic Eurycea which are comparable to the general pattern of morphological adaptation observed in other troglobitic organisms (see Eigenmann, 1909; Poulson, 1963, 1964; Vandel, 1964; Brandon, 1971). Troglobitic invertebrates, fishes, and salamanders are characterized by depigmentation, reduction in eye size, elongation of appendages and hypertrophy of the trophic apparatus in comparison to epigean relatives. In some cases the trunk is shortened as well; in the troglobitic Eurycea the observed reduction in the number of trunk vertebrae (see Table 5) seems to be correlated with a locomotory shift from swimming in swift spring currents to walking in still cave waters. The usual explanation for the common suite of changes observed in troglobites invokes maximization of met-

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Table 5 . Distribution of numbers of trunk vertebrae in 23 population samples of Texas *Eurycea*.

Population	Number of trunk vertebrae					
	13	14	15	16	17	18
Cibolo Creek (epigean)					96	13
Fischer's Well					1	
Bender's Cave				1	79	1
Honey Creek Cave (*E. neotenes*)					6	
Deadman's Cave					7	8
Alzafar Water Cave					12	2
Golden Fawn Cave					1	
Victor Phillip Water Cave				1	19	2
Behr's Cave					4	
Salamander Cave					9	
Haby Water Cave					1	1
Tucker Hollow Cave				3	7	
Carson Cave					15	

Fourmile Cave				8	
Cascade Caverns System			5	8	6	1
Valdina Farms Sinkhole		1	4	20	14	1
Barton Springs			2	35	3	
Honey Creek Cave (*E. tridentifera*)	9	48	3			
Kappelman Salamander Cave		5				
Calmbach Cave		1				
Grosser's Sinkhole	2	14	5			
Badweather Pit	3	43	1			
Elm Springs Cave	1	7				

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abolic efficiency in the energy-poor cave environment (Barr, 1968). Eyes and pigment are reduced to conserve developmental and maintenance costs, appendages are lengthened both to conserve metabolic energy in locomotion and to increase their efficiency as tactile sensors, and the trophic apparatus (particularly in predators) is hypertrophied and specialized to increase feeding efficiency (Poulson and White, 1969).

An analysis of troglobitic adaptation in the Texas Eurycea must contend with the existence of ontogenetic allometry in tooth counts and body proportions; for this reason comparisons among populations must be made in terms of regression analyses. In the present case, variable (and often small) sample sizes and non-normal distributions of individuals within samples make rigorous comparisons of regression statistics among populations relatively insensitive to existing differences, and other means of comparing populations must be derived from the regression equations.

Twenty-two of the 30 known or reported cave-dwelling populations of Eurycea (including two at Honey Creek Cave) are represented by specimens; 18 of these populations are represented by four or more individuals each and are analyzed below. Table 6 presents the results of bivariate correlation and regression analyses of 11 ontogenetically allometric characters against two measures of body size (standard length and axilla-groin length) in the 18 cave-inhabiting populations. All proportional characters are significantly correlated with body size, with the exception of eye diameter,

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which is constant in three advanced troglobitic populations. There is some consistency in the range of slopes among proportional characters; these are generally negatively allometric (mean of 0.93± 0.02) but range from 0.61 to 1.21. Tooth counts are relatively variable, and are less generally correlated with body size than are proportions. Most of the non-significant correlations in premaxillary vomerine, palatopterygoid and dentary tooth counts occur in samples of fewer than 10 individuals; among the larger samples only the Valdina Farms Sinkhole population fails to show significant size dependence in any tooth counts. The numbers of coronoid teeth are not significantly correlated with size in 16 of the 18 populations. This apparently owes to two factors: considerable individual variability, and a tendency for coronoid teeth to increase in number in early ontogeny, then decrease in later ontogeny. The allometric coefficients of tooth counts are less regular than those of body proportions, but are again negatively allometric in general. The mean slope of premaxillary, vomerine, palatopterygoid and dentary teeth regressed on body size is 0.62± 0.07, ranging from 0.18 to 1.44. The numbers of coronoid teeth are in general not correlated with body size owing to the reasons noted above.

As noted previously, variation in sample sizes and size distributions makes detailed analysis of regression statistics among populations an exercise of limited practical value. For the purposes of this section a less rigorous but

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Table 6. Regression statistics for body proportions and tooth counts in 18 samples from troglobitic populations of Texas *Eurycea*. The sequence of presentation follows the text. Symbols are identified on page 239.

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Bender's Cave, Comal County (N = 46)

Variables	r^2	Slope	Intercept
GL/SL	0.80	1.00	0.191
LHL/SL	0.95	0.97	0.308
HW/SL	0.92	1.10	0.107
ED/SL	0.67	0.72	0.076
HLL/SL	0.94	0.94	0.279
AG/SL	0.96	1.05	0.458
PM/SL	0.66	0.96	0.582
VO/SL	0.73	0.74	1.927
PAL/SL	0.54	0.65	2.034
COR/SL	0.25	-0.74	197.970
DEN/SL	0.71	0.72	4.054
HLL/AG	0.89	0.85	0.634

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Honey Creek Cave, Comal County (*Eurycea neotenes*, N = 6)

Variables	r^2	Slope	Intercept
GL/SL	0.93	0.86	0.307
LHL/SL	0.94	0.73	0.648
HW/SL	0.82	0.72	0.397
ED/SL	0.77	0.45	0.268
HLL/SL	0.90	0.75	0.489
AG/SL	1.00	1.16	0.342
PM/SL	0.44*	0.54	2.192
VO/SL	0.70	0.74	1.904
PAL/SL	0.73	0.82	0.931
COR/SL	0.17*	0.26	5.527
DEN/SL	0.54	0.37	10.139
HLL/AG	0.92	0.65	0.969

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Deadman's Cave, Kendall County (N = 15)

Variables	r^2	Slope	Intercept
GL/SL	0.99	0.91	0.247
LHL/SL	0.99	0.91	0.357
HW/SL	0.98	0.97	0.161
ED/SL	0.92	0.68	0.084
HLL/SL	0.97	0.87	0.331
AG/SL	0.99	1.01	0.534
PM/SL	0.86	0.63	1.715
VO/SL	0.94	0.54	3.485
PAL/SL	0.58	0.44	3.427
COR/SL	0.00*	0.01	14.849
DEN/SL	0.94	0.78	2.790
HLL/AG	0.96	0.86	0.581

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Alzafar Water Cave, Kendall County (N = 14)

Variables	r^2	Slope	Intercept
GL/SL	0.94	0.95	0.213
LHL/SL	0.97	0.86	0.429
HW/SL	0.98	0.97	0.172
ED/SL	0.84	0.72	0.077
HLL/SL	0.86	0.78	0.485
AG/SL	0.96	1.01	0.544
PM/SL	0.76	0.47	3.147
VO/SL	0.78	0.39	6.637
PAL/SL	0.01*	0.05	14.345
COR/SL	0.00*	-0.02	15.300
DEN/SL	0.64	0.56	6.375
HLL/AG	0.93	0.79	0.749

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Victor Phillip Water Cave, Kendall County (N = 21)

Variables	r^2	Slope	Intercept
GL/SL	0.90	0.86	0.291
LHL/SL	0.96	0.79	0.502
HW/SL	0.83	0.76	0.320
ED/SL	0.66	0.31	0.262
HLL/SL	0.92	1.00	0.213
AG/SL	0.99	1.10	0.401
PM/SL	0.49	0.50	2.389
VO/SL	0.49	0.59	2.723
PAL/SL	0.33	0.66	1.574
COR/SL	0.06*	-0.23	29.710
DEN/SL	0.17*	0.56	4.374
HLL/AG	0.91	0.89	0.501

Behr's Cave, Kendall County (N = 4)

Variables	r^2	Slope	Intercept
GL/SL	0.99	0.90	0.265
LHL/SL	0.99	0.86	0.436
HW/SL	0.99	0.99	0.163
ED/SL	0.90	0.63	0.121
HLL/SL	0.92	1.10	0.161
AG/SL	0.97	1.04	0.471
PM/SL	0.41*	0.19	8.017
VO/SL	0.70*	0.33	7.896
PAL/SL	0.86	0.70	1.719
COR/SL	0.88	-0.08	34.222
DEN/SL	0.57*	0.27	19.395
HLL/AG	0.99	1.08	0.339

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Salamander Cave, Travis County (N = 5)

Variables	r^2	Slope	Intercept
GL/SL	0.88	0.83	0.376
LHL/SL	0.97	0.93	0.347
HW/SL	0.92	1.19	0.082
ED/SL	0.79	1.34	0.007
HLL/SL	0.94	1.08	0.155
AG/SL	0.98	1.11	0.374
PM/SL	0.84	0.59	1.737
VO/SL	0.99	0.84	1.213
PAL/SL	0.04*	0.35	3.030
COR/SL	0.12*	-0.37	49.865
DEN/SL	0.65	0.51	7.335
HLL/AG	0.98	0.99	0.387

Tucker Hollow Cave, Real County (N = 9)

Variables	r^2	Slope	Intercept
GL/SL	0.99	1.09	0.144
LHL/SL	0.94	0.75	0.633
HW/SL	0.99	1.05	0.140
ED/SL	0.99	0.58	0.125
HLL/SL	0.98	0.99	0.215
AG/SL	0.99	1.02	0.550
PM/SL	0.90	0.53	2.677
VO/SL	0.70	0.43	4.740
PAL/SL	0.76	0.39	4.587
COR/SL	0.33*	-0.52	61.645
DEN/SL	0.71	0.80	2.647
HLL/AG	0.98	0.97	0.387

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Carson Cave, Uvalde County (N = 15)

Variables	r^2	Slope	Intercept
GL/SL	0.98	0.87	0.278
LHL/SL	0.97	0.88	0.383
HW/SL	0.98	0.90	0.216
ED/SL	0.60	0.51	0.129
HLL/SL	0.97	1.14	0.138
AG/SL	0.99	1.15	0.333
PM/SL	0.89	0.84	0.865
VO/SL	0.71	0.57	2.794
PAL/SL	0.40	0.36	4.391
COR/SL	0.00*	0.01	14.391
DEN/SL	0.76	0.48	7.343
HLL/AG	0.96	0.98	0.420

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Fourmile Cave, Val Verde County (N = 8)

Variables	r^2	Slope	Intercept
GL/SL	0.91	0.98	0.204
LHL/SL	0.97	0.94	0.329
HW/SL	0.93	1.02	0.128
ED/SL	0.59	0.71	0.074
HLL/SL	0.87	1.12	0.159
AG/SL	0.95	1.21	0.254
PM/SL	0.31*	0.73	1.205
VO/SL	0.11*	0.23	10.111
PAL/SL	0.14*	1.37	0.114
COR/SL	0.13*	1.19	0.117
DEN/SL	0.83	0.95	1.577
HLL/AG	0.86	0.90	0.617

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Cascade Caverns and Cascade Sinkhole, Kendall County (N = 17)

Variables	r^2	Slope	Intercept
GL/SL	0.97	0.94	0.236
LHL/SL	0.95	0.83	0.476
HW/SL	0.95	0.99	0.168
ED/SL	0.85	0.78	0.053
HLL/SL	0.95	1.01	0.206
AG/SL	0.97	1.16	0.310
PM/SL	0.36	0.34	4.367
VO/SL	0.52	0.35	7.468
PAL/SL	0.53	0.29	6.045
COR/SL	0.00*	0.00	14.028
DEN/SL	0.81	0.47	8.346
HLL/AG	0.95	0.86	0.598

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Valdina Farms Sinkhole, Medina County (N = 38)

Variables	r^2	Slope	Intercept
GL/SL	0.76	0.94	0.262
LHL/SL	0.77	0.83	0.542
HW/SL	0.75	0.96	0.203
ED/SL	0.48	1.41	0.006
HLL/SL	0.55	0.60	1.075
AG/SL	0.92	1.14	0.374
PM/SL	0.02*	0.20	11.050
VO/SL	0.00*	0.03	25.480
PAL/SL	0.00*	-0.07	23.324
COR/SL	0.02*	-0.54	92.193
DEN/SL	0.16*	0.36	13.877
HLL/AG	0.45	0.46	2.352

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Barton Springs, Travis County (N = 34)

Variables	r^2	Slope	Intercept
GL/SL	0.89	0.89	0.260
LHL/SL	0.96	0.82	0.472
HW/SL	0.90	0.83	0.270
ED/SL	0.43	0.53	0.126
HLL/SL	0.87	0.89	0.341
AG/SL	0.98	1.14	0.344
PM/SL	0.48	0.54	2.598
VO/SL	0.70	0.59	3.404
PAL/SL	0.46	0.63	1.821
COR/SL	0.02*	0.13	12.317
DEN/SL	0.48	0.49	7.596
HLL/AG	0.84	0.75	0.830

Honey Creek Cave, Comal County (*E. tridentifera*, N = 38)

Variables	r^2	Slope	Intercept
GL/SL	0.72	0.90	0.336
LHL/SL	0.91	0.84	0.576
HW/SL	0.83	0.99	0.211
ED/SL	0.08	0.46	0.094
HLL/SL	0.73	0.69	0.842
AG/SL	0.85	1.12	0.349
PM/SL	0.28	0.77	1.456
VO/SL	0.22	0.54	4.969
PAL/SL	0.11	0.42	5.419
COR/SL	0.00*	-0.09	25.404
DEN/SL	0.32	0.59	6.625
HLL/AG	0.56	0.50	2.214

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Kappelman Salamander Cave, Comal County (N = 4)

Variables	r^2	Slope	Intercept
GL/SL	0.99	0.88	0.352
LHL/SL	0.99	0.94	0.401
HW/SL	0.97	0.98	0.226
ED/SL	0.80	0.50	0.079
HLL/SL	0.83	0.61	1.053
AG/SL	0.99	1.06	0.439
PM/SL	0.28*	0.59	2.917
VO/SL	0.68*	1.07	0.678
PAL/SL	0.04*	0.18	12.416
COR/SL	0.48*	-1.56	2265.687
DEN/SL	0.23*	1.44	0.266
HLL/AG	0.77*	0.55	1.805

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Grosser's Sinkhole, Comal County (N = 17)

Variables	r^2	Slope	Intercept
GL/SL	0.64	0.78	0.461
LHL/SL	0.81	0.75	0.760
HW/SL	0.74	0.86	0.298
ED/SL	0.04*	0.36	0.148
HLL/SL	0.78	0.90	0.399
AG/SL	0.91	1.11	0.369
PM/SL	0.00*	0.06	15.951
VO/SL	0.17	0.39	8.377
PAL/SL	0.02*	0.18	12.488
COR/SL	0.06*	-0.38	80.094
DEN/SL	0.57	0.75	3.742
HLL/AG	0.79	0.78	0.971

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Badweather Pit, Comal County (N = 37)

Variables	r^2	Slope	Intercept
GL/SL	0.86	0.95	0.278
LHL/SL	0.95	0.82	0.613
HW/SL	0.92	1.02	0.199
ED/SL	0.00*	-0.02	0.536
HLL/SL	0.86	0.71	0.774
AG/SL	0.94	0.98	0.571
PM/SL	0.69	0.96	0.722
VO/SL	0.52	0.74	2.298
PAL/SL	0.13	0.31	7.010
COR/SL	0.08	-0.85	198.609
DEN/SL	0.51	0.50	8.838
HLL/AG	0.78	0.67	1.355

Elm Springs Cave, Bexar County (N = 8)

Variables	r^2	Slope	Intercept
GL/SL	0.71	0.77	0.510
LHL/SL	0.83	0.81	0.611
HW/SL	0.72	0.77	0.427
ED/SL	0.01*	-0.14	0.728
HLL/SL	0.71	0.63	1.030
AG/SL	0.95	1.04	0.454
PM/SL	0.61	1.35	0.171
VO/SL	0.82	0.99	1.062
PAL/SL	0.64	1.27	0.281
COR/SL	0.05*	-0.43	57.943
DEN/SL	0.76	0.90	2.294
HLL/AG	0.73	0.60	1.698

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more readily interpretable comparative method can be derived from regression equations, by solving them for a single, uniform body size to yield "standardized" representatives of each population (Lynch and Wake, 1975). Ideally this size should be close to the sample mean size, but this is not practical in the Texas Eurycea because the mean size of individuals varies considerably among populations. A value of 38.0 mm in standard length was selected as a base value; this is close to the maximum known size in several populations but well within the adult size range of the majority. In either case the amount of error introduced by examining animals of potentially different ages is relatively small, since most proportions and tooth counts scale nearly isometrically with body size (Table 6).

The body proportions and numbers of teeth for standardized representatives of each of the 18 populations are listed in Table 7 . Also listed is the mean number of trunk vertebrae in each population sample; the distribution of numbers of trunk vertebrae among populations is presented in Table 5 . Table 8 provides measurements and tooth counts for five specimens representing four populations not analyzed in Table 7 .

Tables 7 and 8 demonstrate the degree of morphological variation present among troglobitic populations of the Texas Eurycea. Mean trunk vertebral number decreases from 17.5 to 13.9, eye diameter decreases by a factor of 3, and hind limb length, number of premaxillary, vomerine, palato-

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Table 7 . Mean trunk vertebral numbers and standardized character states for 38.0 mm individuals from 18 troglobitic populations of Texas *Eurycea*. Symbols are identified at the end of this table. Underlined values are estimates from correlations lacking statistical significance.

Population	$\overline{TV}$	SL	GL	LHL	HW	ED	HLL	AG	PM	VO	PAL	COR	DEN
Bender's Cave	17.0	38.0	7.3	10.5	5.9	1.0	8.5	20.9	19	28	22	13	56
Honey Creek Cave (*E. neotenes*)	17.0	38.0	7.0	9.2	5.4	1.4	7.5	23.3	16	28	18	14	39
Deadman's Cave	17.5	38.0	6.8	9.8	5.5	1.0	7.8	21.0	17	25	17	15	48
Alzafar Water Cave	17.2	38.0	6.8	9.8	5.8	1.0	8.3	21.4	17	27	17	15	49
Victor Phillip Water Cave	17.0	38.0	6.6	8.9	5.1	1.0	8.1	21.9	15	23	17	13	34
Behr's Cave	16.8	38.0	7.0	10.0	6.0	1.2	8.8	20.7	16	26	22	26	52
Salamander Cave	17.0	38.0	7.7	10.2	6.2	1.0	7.9	21.2	17	26	11	13	50

Tucker Hollow Cave	16.7	38.0	7.6	9.7	6.4	1.0	7.9	22.5	18	23	19	9	49
Carson Cave	17.0	38.0	6.6	9.4	5.7	0.8	8.8	21.8	18	22	16	15	42
Fourmile Cave	17.0	38.0	7.2	10.0	6.0	1.0	9.4	20.8	17	23	17	9	50
Cascade Caverns & Sinkhole	16.2	38.0	7.2	9.7	6.2	0.9	8.1	21.1	15	27	17	14	46
Valdina Farms Sinkhole	16.2	38.0	8.0	11.1	6.7	0.4	9.5	21.3	23	28	18	13	51
Barton Springs	16.0	38.0	6.6	9.3	5.5	0.9	8.7	21.8	18	29	18	20	45
Honey Creek Cave (*E. tridentifera*)	13.9	38.0	8.9	12.2	7.7	0.5	10.4	20.5	24	35	25	18	57
Kappelman Salamander Cave	14.0	38.0	8.6	12.2	8.0	0.5	9.7	20.7	25	33	24	8	50
Grosser's Sinkhole	14.1	38.0	7.9	11.6	6.8	0.5	10.5	20.9	20	35	24	20	57
Badweather Pit	14.0	38.0	8.8	12.1	8.1	0.5	10.2	20.2	24	34	22	13	54
Elm Springs Cave	13.9	38.0	8.4	11.6	7.0	0.4	10.2	18.6	23	39	28	12	61

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SYMBOLS:

$\overline{TV}$: mean number of trunk vertebrae (see Table 5)

SL: standard length (tip of snout to posterior margin of cloaca)

GL: gular length (tip of snout to gular fold at ventral midline)

LHL: linear head length (tip of snout to base of third gill ramus)

HW: head width (span between jaw articulations)

ED: eye diameter (measured transversely under strong backlighting

HLL: hind limb length (groin to tip of longest toe)

AG: axilla-groin length

PM, VO, PAL, COR, DEN: Premaxillary, vomerine, palatopterygoid, coronoid and dentary teeth (counts combine left and right sides)

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Table 8. Counts and measurements for 5 specimens of troglobitic *Eurycea* representing populations not analyzed by regressions. Symbols as in Table 7.

Population	TV	SL	GL	LHL	HW	ED	HLL	AG	PM	VO	PAL	COR	DEN
Fischer's Well	17	34.0	6.5	7.5	5.3	0.8	7.0	19.5	13	22	16	20	41
Golden Fawn Cave	17	37.7	7.5	10.0	5.7	1.2	8.0	20.4	15	25	16	16	48
Haby Water	18	36.4	6.4	8.4	5.5	1.0	7.1	20.2	14	21	16	16	44
Cave	17	39.0	7.5	10.4	6.5	1.3	7.4	20.5	19	26	13	9	48
Calmbach Cave	14	30.0	6.5	9.6	5.7	0.3	9.0	19.0	16	26	23	20	53

pterygoid and dentary teeth, and measures of head size generally increase in increasingly cave-adapted populations. It is interesting to note that axilla-groin length does not decrease in direct proportion with the decreasing number of trunk vertebrae: axilla-groin length decreases 6.5% between the six populations having means of 17.0-17.5 trunk vertebare and the five populations having means of 13.9-14.1 trunk vertebrae; the corresponding decrease in average mean vertebral number is 18.2%.

Information of a second kind is available from the data in Table 7 : how closely correlated are the observed trends in character states within population? Since troglobitic animals in general display a similar suite of adaptations, it might be argued that this suite is under rather strong selective control as a unit, and thus that the state of any one character is a good predictor of the states of the remaining characters. Alternatively, trophic and locomotor character suites may be analyzed separately with the same question in mind. An appropriate method for this analysis involves a modification of Kendall's coefficient of concordance (Siegel, 1956). As usually employed, this non-parametric technique evaluates the degree of agreement (from 0 to 1) among rankings of individuals by several judges. Here the degree of agreement among populations in rankings by character states can serve as a measure of the concordance of character state trends within the troglobitic Eurycea. The coefficient of concordance is a ranking test (a more de-

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tailed discussion of this technique is presented in introducing a measure of hybridization in Chapter VI); thus in application to the data of Table 7 two characters which are not amenable to ranking must be rejected. Standard length is a constant in this data set, and the numbers of coronoid teeth do not differ appreciably between populations rank-ordered high and low on the basis of the remaining character states. The mean number of coronoid teeth for the five "least cave-adapted" populations (Victor Phillip Water Cave, Honey Creek Cave *E. neotenes*, Deadman's Cave, Carson Cave, and Alzafar Water Cave) is 14.5 (range of 13-15); the corresponding figure for the five "most cave-adapted" populations (Grosser's Sinkhole, Kappelman Salamander Cave, Elm Springs Cave, Badweather Pit, and Honey Creek Cave *E. tridentifera*) is 14.2 (range of 8-20). (Populations of ranks 6-12 in this analysis are as follows: Salamander Cave and Tucker Hollow [tied], Cascade Caverns System, Barton Springs, Fourmile Cave, Behr's Cave, Bender's Cave, and Valdina Farms Sinkhole.)

Kendall's coefficient of concordance for the 18 populations on the basis of 11 characters is 0.656 (with correction for tied scores). In isolation, this figure is not meaningful. Values of 0.500-0.940 are reported in Chapter VI for the agreement among a similar set of characters within populations of epigean and troglobitic *Eurycea*; in comparison the value of 0.656 is not particularly high, and might be taken as an indication that while a moderate amount

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of predictability or concordance exists within the suite of characters showing directional change in increasingly troglobitic populations, the suite contains a considerable amount of variability.

If the analysis is restricted in scope to "trophic" (GL, LHL, HW, PM, VO, PAL, DEN), or "locomotor" adaptations (TV, HLL, AG) the picture changes slightly. The concordance of trophic structures is 0.801, and the concordance of locomotor adaptations is 0.744. The three concordance values are highly significant (non random) by chi square tests, as detailed in Siegel (1956, p. 236). The Spearman rank correlation between the trophic and locomotor scores is 0.89. From these analyses it appears that trends in the morphology of trophic structures may be more narrowly circumscribed than trends in locomotor adaptations, and that the two sets of adaptations are closely correlated in troglobitic populations of Eurycea.

Groupings of Adaptive Grades

It is apparent from the fact that most populations of troglobitic Eurycea inhabit small, isolated cave systems that many of these populations represent independent colonizations of cave environments. Only the populations of the Guadalupe valley, and particularly those of the Cibolo Sinkhole Plain and its environs, appear to inhabit cave systems having reasonable possibilities of physical continuity. Most or all of the other troglobitic populations are mutually isolated, and are thus evolving in parallel; existing

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similarities represent independent population responses to similar selective regimes. Morphologically comparable but widely separated populations thus comprise adaptive grades rather than clades. With this in mind, phenetic grouping techniques may be employed to identify and distinguish among adaptive grades, if any exist. The results of the preceding section demonstrates that this type of analysis may be useful in understanding the adaptive trends in troglobitic populations.

An extremely conservative (and hence robust) grouping technique can be derived from discriminant analysis. This method seeks to maximize the differentiation among specified sets through the construction of a series of orthogonal linear functions composed of weighted character states. Its usual purpose is to discriminate rather than to affiliate however, when the method fails in discrimination it becomes a robust measure of the similarity of sets. The degree of success or failure of the discriminant functions can be evaluated through application of a posteriori classification functions derived from them. Individuals are classified into the specified sets on the basis of their positions in discriminant space; depending on the degree of discrimination possible among sets, a variable number of individuals may be misclassified into sets other than their assigned set. A measure of the degree and direction of the affiliation among sets can be derived from the distribution of these misclassified individuals. More inclusive subgroup-

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ings of sets within the total sample can be constructed in this way, and their validity as mutually exclusive units can be evaluated by deriving a second series of discriminant functions. This stepwise procedure permits the use of discriminant functions as both a grouping and an isolating technique.

A discriminant analysis was performed on 22 population samples of cave-dwelling Eurycea, with one wholly epigean population sample added for comparative purposes. The set of 13 variables previously used (Table 6) was again employed. The prior probabilities of sample membership were defined as equal, rather than being tied to differences in sample sizes. This action permits misclassification on a uniform basis throughout the data set, a desirable feature in the use of discriminant functions as a group-finding procedure.

The first three functions in this 23-set analysis explain 89.9% of the total sample variance; a 95% level of explanation requires six functions. The six largest discriminant coefficients (weighting values) loading on each of the first three orthogonal axes are listed in Table 9 ; body size, proportional characters and numbers of trunk vertebrae are more effective discriminators than are tooth counts. The posterior probability classification routine derived from the first six functions results in the correct allocation of 66% of the included individuals to their known populations (with a range of 14-100%).

A substantial number of individuals are misclassified

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Table 9. The six largest character loadings for the first three discriminant functions in the 23 group discriminant analysis. Percents of explained variance noted.

Function 1 (76.9%)		Function 2 (8.6%)		Function 3 (4.3%)	
Character	Coefficient	Character	Coefficient	Character	Coefficient
TV	0.464	LHL	-2.018	HW	1.847
SL	0.446	AG	1.062	SL	-1.302
LHL	-0.266	TV	-1.016	PM	0.681
HLL	-0.247	HLL	-0.702	HLL	0.620
ED	0.229	SL	0.662	VO	-0.501
HW	-0.125	GL	0.531	ED	0.440

in this analysis, permitting an attempt to define subgroups or adaptive grades of similar populations within the data set. Several such subgroups are apparent in the data matrix if the grouping criterion is arbitrarily set at inclusion of at least 75% of the individuals in each population. Small samples pose a problem in allocation, since those with six or fewer individuals generally do not show misclassifications. These samples were not allowed to stand as independent subgroups, but were included in the subgroup whose members were most frequently misclassified into them. In other words, in all cases in this analysis some individuals from other populations were incorrectly predicted to be members of another population of small sample size. This misclassification was taken as evidence that the latter population was sufficiently similar to other populations of a cohesive subgroup to be included in that unit.

With these restrictions the most parsimonious grouping arrangement involves the recognition of five in the set of 23 populations. The epigean sample and the Barton Springs population represent two sharply-defined single-population subgroups; the posterior probability functions correctly predict 81.6% and 85.3%, respectively, of their actual memberships. Three subgroups (consisting of nine, six and six populations) contain the remaining samples (Table 10). One subgroup is composed of the eight incipient troglobitic populations occurring in the Guadalupe valley (excluding *E. tridentifera* of Honey Creek Cave), and *E. latitans* of the

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Table 10. Actual and predicted compositions of three subgroups of troglobitic *Eurycea* generated by the pattern of misclassification of individuals in discriminant analyses. The diagonal of the table indicates the number of correctly allocated specimens; other column entries denote misclassified specimens. The last column shows the percent of individuals from each population which are assigned to the subgroup as a whole.

	GUADALUPE SUBGROUP										
Actual Population		Predicted Membership									
	N	FW	BnC	HCCN	DC	AWC	GFC	VPWC	BhC	CCS	%
Fisher Well	1	1	-	-	-	-	-	-	-	-	100
Bender's Cave	46	-	27	-	3	3	2	-	4	-	84.8
Honey Creek Cave (*E. neotenes*)	6	-	-	6	-	-	-	-	-	-	100
Deadman's Cave	15	-	1	-	10	2	-	-	-	-	86.7
Alzafar Water Cave	14	1	3	1	1	2	2	-	1	-	78.6
Golden Fawn Cave	1	-	-	-	-	-	1	-	-	-	100
Victor Phillip Water Cave	13	-	-	1	1	-	-	10	-	-	92.3
Behr's Cave	4	-	-	-	-	-	-	-	4	-	100
Cascade Caverns System	17	2	1	-	1	1	-	1	-	10	94.1

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DISPERSED SUBGROUP

Actual Population		Predicted Membership						
	N	SC	VFS	HWC	THC	CC	FC	%
Salamander Cave	5	3	-	1	-	1	-	100
Valdina Farms Sinkhole	38	2	24	-	1	1	4	84.2
Haby Water Cave	2	-	-	2	-	-	-	100
Tucker Hollow Cave	9	-	-	-	6	-	1	77.7
Carson Cave	15	1	-	-	1	11	1	93.3
Fourmile Cave	8	2	-	-	-	-	4	75.0

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TRIDENTIFERA SUBGROUP

Actual Population		Predicted Membership						
	N	HCCT	KSC	CC	GS	BP	ESC	%
Honey Creek Cave (*E. tridentifera*)	38	22	-	1	6	1	8	100
Kappelman Salamander Cave	4	-	2	-	-	1	1	100
Calmbach Cave	1	-	-	1	-	-	-	100
Grosser's Sinkhole	17	5	-	-	10	-	2	100
Badweather Pit	37	4	4	-	1	21	7	100
Elm Springs Cave	8	1	1	-	-	-	6	100

Cascade Caverns System of the western Cibolo Sinkhole Plain. This assemblage is hereafter referred to as the Guadalupe Subgroup; the posterior probability functions correctly predict 88.0% of its actual membership of individuals. A second definable subgroup consists of six troglobitic populations distributed across the southern Edwards Plateau; this is termed the Dispersed Subgroup. As defined (Table 10), 89.6% of its actual membership is correctly predicted. A third subgroup is composed of the six populations I have previously referred to E. tridentifera (Sweet, 1977b), and is here termed the Tridentifera Subgroup. Predicted membership is 100% of actual membership.

A second discriminant analysis involving these five subgroups provides a test of the validity of this partitioning arrangement. Here the purpose of the analysis is to discriminate among subgroups; if these subgroups accurately reflect adaptive grades the number of misclassified individuals should be substantially reduced in comparison to the level of misclassification (34%) observed in the initial 23-population analysis. Such a reduction would indicate that members of these subgroups share features not common to other subgroups. Two discriminant functions are required to explain 95% of the total sample variance (90.4% and 5.6%) in the five-subgroup analysis; the posterior probability functions correctly allocate 73.3% of actual subgroup memberships (Table 11). This grouping results in only a small improvement in the number of misclassified individuals (26.7%

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vs. 34%). The Epigean, Barton and Tridentifera Subgroups retain their distinctiveness, but the Guadalupe Subgroup overlaps extensively with both the Epigean and Dispersed Subgroups, and the Dispersed Subgroup overlaps with the Guadalupe Subgroup (Table 11).

An examination of the distribution of misclassified individuals among populations comprising each subgroup shows that 17 of the 24 Guadalupe subgroup members incorrectly allocated to the Epigean Subgroup occur in the Fischer Well (1/1), Honey Creek Cave (5/6) and Victor Phillip Water Cave (11/13) samples. The remaining misclassified individuals represent small minorities of their actual populations. The overlap between the Guadalupe and Dispersed Subgroups is chiefly the result of 19 misclassified specimens (of 46) in the Bender's Cave population. Individuals of the Dispersed Subgroup misclassified into the Guadalupe Subgroup occur in all populations; however, fully 30 of the 43 correctly allocated specimens are from the Valdina Farms Sinkhole population. The pattern of overlap and misclassification seen among the Epigean, Guadalupe and Dispersed Subgroups suggests that modifications involving these three units may result in a better overall partitioning of adaptive grades in the Texas Eurycea. In keeping with this pattern, the Fischer Well, Honey Creek Cave and Victor Phillip Water Cave populations were shifted to the Epigean Subgroup, and the Valdina Farms Sinkhole population was defined as a new subgroup (the Troglodytes Subgroup); the remaining populations

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of the Guadalupe and Dispersed Subgroups were then merged into a single Intermediate Subgroup. Transfer of the Fischer Well, Honey Creek Cave, and Victor Phillip Water Cave populations to the Epigean Subgroup is consistent with the observation that members of these populations inhabit both surface and subterranean waters; a more detailed analysis of the differing degrees of troglobitic adaptation present in the populations of the Guadalupe valley is presented in Chapter VI. The merger of other populations of the Guadalupe and Dispersed Subgroups seems warranted on the basis of misclassifications in the five-subgroup analysis, though the two subgroups are distinguishable at the level of the 23-population discrimination.

When these subgroups (Epigean, Barton, Intermediate, Troglodytes and Tridentifera) are redefined, a third series of discriminant analyses serves to evaluate the resulting degree of improvement in differentiability. Two functions are required to exceed the 95% level of explained variance (89.7% and 6.4%) in this data set. The posterior probability functions of this analysis correctly predict the allocation of 86.6% of individuals to their assigned subgroups (Table 11). The Barton, Tridentifera, and reconstituted Epigean Subgroups are clearly demarcated, with 91.2%, 100% and 98.6% correct classifications, respectively. The Intermediate and Troglodytes Subgroups are moderately well-defined (72.8% and 73.7% correct allocations). The wide distribution of misclassified individuals among the populations comprising the

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Table 11. Actual and predicted compositions of potential adaptive grades among populations of Texas *Eurycea*, as discussed in the text.

FIRST FIVE-SUBGROUP ANALYSIS						
Defined Subgroup		Predicted Membership				
	N	EPIG	BART	GUAD	DISP	TRID
Epigean	49	47	-	2	-	-
Barton	34	1	31	2	-	-
Guadalupe	117	24	13	54	26	-
Dispersed	77	4	5	22	43	3
Tridentifera	105	-	-	-	-	105

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SECOND FIVE-SUBGROUP ANALYSIS

Defined Subgroup		Predicted Membership				
	N	EPIG	BART	INT	TROG	TRID
Epigean	69	68	1	-	-	-
Barton	34	1	31	2	-	-
Intermediate	136	15	14	99	8	-
Troglodytes	38	-	1	6	28	3
Tridentifera	105	-	-	-	-	105

Intermediate Subgroup suggests that little improvement is possible by further removal or addition of populations, since misclassified individuals are scattered throughout the included populations. The Troglodytes Subgroup cannot be further subdivided, nor can it be grouped with other populations; misclassifications apparently result from the extreme variability of individuals comprising the Valdina Farms Sinkhole population. The basis for this heterogeneity, unique in the Texas *Eurycea*, is examined in Chapter VI.

CONCLUSIONS

General considerations

The results of the preceding section and of this series of discriminant analyses can be summarized in eight statements concerning the recognition, composition, and distinguishability of subgroups in the Texas *Eurycea*.

1) Proportional and meristic characters show consistent trends within troglobitic populations. As a group the characters are moderately concordant among populations; trophic specializations are more nearly concordant than locomotor adaptations, and both are as concordant as character states *within* most single populations of epigean and troglobitic *Eurycea* (see Chapter VI).

2) The Cibolo Creek headwaters population, representative of epigean samples of *Eurycea neotenes*, is differentiable from most troglobitic populations of *Eurycea*.

3) Three cave-associated populations (Fischer's Well, Honey Creek Cave *E. neotenes*, and Victor Phillip Water Cave)

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of the Guadalupe valley show strong affinities to the Cibolo Creek population; all four are best regarded as representing an Epigean Subgroup of minimal troglobitic adaptation.

4) Eleven fully troglobitic populations (Bender's Cave, Deadman's Cave, Alzafar Water Cave, Golden Fawn Cave, Behr's Cave, Cascade Caverns System, Salamander Cave, Haby Water Cave, Tucker Hollow Cave, Carson Cave and Fourmile Cave) comprise an Intermediate Subgroup of incipient to moderate levels of troglobitic adaptation. These populations cannot represent a monophyletic assemblage by virtue of their occurrence in small, isolated cave systems distributed across the southern margin of the Edwards Plateau; similarities among them are the result of parallel evolution rather than common ancestry.

5) Eurycea latitans of the Cascade Caverns System is a member of the Intermediate Subgroup, despite its proximity to populations of E. tridentifera in the Cibolo Sinkhole Plain and geologic evidence suggesting that the Cascade Caverns System is a tributary of the Cibolo Sinkhole Plain subterranean system.

6) The Barton Springs population is consistently separable from all other populations and subgroups examined. It represents a moderately advanced stage of troglobitic adaptation, and fits into an otherwise unoccupied position between intermediate and advanced troglobitic Eurycea.

7) Eurycea troglodytes of Valdina Farms Sinkhole is differentiable from other troglobitic populations, but is com-

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prised of a heterogeneous array of morphotypes.

8) The six populations of the advanced troglobite Eurycea tridentifera form a cohesive and well-differentiated subgroup at all levels of analysis. No member of the Tridentifera Subgroup was misclassified into another subgroup in either the 23 population analysis or the two five-group analyses. However, three specimens of Eurycea troglodytes were consistently misclassified as members of the Tridentifera Subgroup in all analyses; as detailed in Chapter VI, these three specimens may actually be individuals of Eurycea tridentifera. Within populations comprising the Tridentifera Subgroup, geologic evidence strongly suggests that the four known populations in tributary caves of the Cibolo Sinkhole Plain are potentially in contact. While the caves of the Cibolo Sinkhole Plain have not been demonstrated to be interconnected by direct examination, they behave as a hydrologic unit with rapid equilibration characteristics. This is generally accepted as evidence of free communication in determining the degree of isolation or continuity of potential components of subterranean drainage networks. The two outlying populations of the Tridentifera Subgroup (Honey Creek Cave and Elm Springs Cave) are not separable by discriminant methods from those of the Cibolo Sinkhole Plain (Table 10), and cannot be argued to be independently-derived populations on geological grounds. The Tridentifera Subgroup is thus best interpreted as a monophyletic unit consisting of a lineage

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of advanced troglobitic salamanders which may have colonized the cave environment at a considerably earlier time than did the ancestral stocks of populations comprising the Intermediate Subgroup.

Systematic Interpretations

Previous work on the Texas Eurycea has resulted in the recognition of six species: E. neotenes, E. pterophila, E. nana, E. latitans, E. troglodytes and E. tridentifera. Both E. pterophila and E. nana are highly restricted in distribution: E. pterophila occupies a single small spring within the range of E. neotenes, and is of doubtful validity (see Chapter VII); E. nana occurs in two large springs in the Balcones Fault Zone on the eastern limb of the plateau (see Chapter III). The remaining named species are either of broad epigean distribution (E. neotenes), or are troglobitic; E. latitans, E. troglodytes and E. tridentifera were each known from a single population at the time of description. Eurycea latitans and E. troglodytes remain as single populations, though some authors have allocated the Deadman's Cave-Century Caverns system population to E. latitans (Baker, 1961; Reddell, 1967b) without explanation. This interpretation is almost certainly incorrect, and is apparently based on the occasional occurrence of specimens in the Deadman's-Century system which are rather pale in color and thus superficially resemble specimens of Eurycea latitans. The remaining troglobitic pop-

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ulations have been frequently cited as representing unnamed taxa (e.g. Reddell, 1967b, 1971; Mitchell and Smith, 1972). These new species were to be five, represented by the Salamander Cave, Bender's Cave, Badweather Pit, Carson Cave, and Fourmile Cave populations (James R. Reddell, personal communication, 1974). The present analysis does not support such action; the Badweather Pit population is clearly a member of the Tridentifera Subgroup, and the remaining four populations are not consistently differentiable either from one another or from the remaining populations with which they constitute the Intermediate Subgroup (Tables 6 and 7).

I have previously concluded (Sweet, 1977b) that six populations showing advanced troglobitic specializations are referable to Eurycea tridentifera Mitchell and Reddell, 1965; this conclusion is supported by the results of the preceding analyses. The morphometric analyses give no indication of structural heterogeneity among these populations, and the geologic evidence is largely consistent with, and certainly does not preclude, the interpretation that the caves inhabited by these populations are components of a more or less interconnected regional system. Eurycea tridentifera is thus known to occur in six caves: Honey Creek Cave, Kappelman Salamander Cave, Calmbach Cave, Grosser's Sinkhole, Badweather Pit, and Elm Springs Cave.

The species allocations of the remaining troglobitic populations are relatively straightforward on the basis of

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the analyses in this chapter. Eurycea troglodytes Baker, 1957, here appears as a morphologically distinctive population which seemingly warrants species status. Several features of this population are unusual in comparison to others of the Texas Eurycea, including a remarkably broad range in coloration (from dark brown to nearly white), a range of 14-18 in trunk vertebral numbers without a strong mode (Table 5), and a lack of statistically significant size-dependence in any tooth counts (Table 6). Additional evidence regarding the taxonomic status of this population is presented in Chapter VI. The Barton Springs population is also clearly distinguishable from others of the Texas Eurycea in body proportions, trunk vertebral numbers, tooth counts and coloration. A description of this population as a new species is in preparation. The Fisher's Well, Honey Creek Cave (dark morph) and Victor Phillip Water Cave populations have been shown to be closely similar to an epigean population assigned to Eurycea neotenes, and are here referred to that species. The remaining populations, members of the Intermediate Subgroup, represent a number of independent lineages evolving in parallel and thus constitute a grade rather than a monophyletic lineage of troglobites. It would be inappropriate to recognize this polyphyletic assemblage as a single species (for which the name Eurycea latitans Smith and Potter, 1946, is technically available). Rather, each population would have to be described as a separate taxonomic entity. This course of

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action would obscure the simplicity of the model here proposed for the origin of troglobitic populations, and in any case is not warranted by the analyses presented above. These populations are sufficiently similar in morphology to Eurycea neotenes to have been derived from that species in the recent past (see Chapter V). Therefore, I propose that the definition of Eurycea neotenes Bishop and Wright, 1937, be expanded to include the incipient and intermediate troglobitic populations of the Intermediate Subgroup. This action relegates the name Eurycea latitans Smith and Potter, 1946, to the synonymy of Eurycea neotenes (see also Chapter VI), and maintains monophyly as a criterion in the systematics of the Texas Eurycea.

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Numerous landowners gave permission to work in caves on their property, and some did not; to both groups I am

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CHAPTER V

NATURAL METAMORPHOSIS IN *EURYCEA NEOTENES*, AND THE GENERIC ALLOCATION OF THE TEXAS *EURYCEA* (AMPHIBIA: PLETHODONTIDAE)

Introduction

The abundant springs and shaded canyons of the Edwards Plateau of central Texas comprise an outpost of mesic conditions in an otherwise relatively arid region. Disjunct, relict populations of hemidactyliine plethodontid salamanders occupy the cool and reliable surface and cave waters of the marginal drainages of the Plateau, which has become the center for a small adaptive radiation in this group (Wake, 1966). As is commonly the case among ambystomatoid salamanders inhabiting marginal environments, the hemidactyliines of the Edwards Plateau are paedogenetic. The normal pattern of metamorphosis to a semiterrestrial adult stage has been suppressed, with sexual maturity attained in aquatic larval morphology. These salamanders, members of the genera *Eurycea* and *Typhlomolge*, have been considered to be obligate paedogenes (Kezer, 1952; Dundee and Gorbman, 1960; Dent, 1968) which respond in varying degrees to the experimental induction of metamorphosis. Following treatment with thyroxin, *T. rathbuni* (Dundee, 1957) and *E. tridentifera* (Wake, 1966; Bogart, 1967) undergo limited metamorphic changes in external and skeletal morphology, but do not transform, whereas *E. neotenes* (Kezer, 1952) and *E. nana*

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(Potter and Rabb, 1960) appear to complete metamorphosis on the basis of external morphology. In addition to these accounts of induced metamorphosis, there are two brief reports of naturally metamorphosed individuals in populations of E. neotenes (Bogart, 1967; Bruce, 1976). In the course of five summers of fieldwork on the Edwards Plateau several populations of E. neotenes have been found which contain a proportion of metamorphosed individuals; the present account documents the occurrence and distribution of these metamorphosing populations, and describes and figures naturally transformed E. neotenes.

The allocation of surface populations of the central Texas paedogenes to Eurycea initially made by Bishop and Wright (1937) has been followed by subsequent authors. This allocation was made on the basis of larval external morphology alone, and has not received critical attention; that the Texas Eurycea may in fact be species of Typhlotriton or some other, possibly undiagnosed, hemidactyliine genus has not been considered previously, but is a distinct possibility. The availability of non-larval specimens of a member of this group facilitates evaluation of its generic status, in that detailed analyses of adult morphology are available for all genera of hemidactyliine plethodontids (Wake, 1966, osteology; Lombard and Wake, 1976, 1977, tongue morphology). Information of this scope is not presently available for hemidactyliine larvae. A detailed description of the morphology of transformed E. neotenes thus broadens

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the definition of this species, and permits the resolution of the question of generic allocation, which can be broadened to encompass the several troglobitic populations thought to be derived from surface stocks (Baker, 1961; Sweet, 1977).

Methods and Materials

Fieldwork was conducted in June 1969, June and July 1970, July and August 1971, and June through September 1973 and 1974. A total of 85 populations was sampled during this period, most on several occasions. All of this material is catalogued in the Museum of Vertebrate Zoology, University of California, Berkeley. Additional material of E. neotenes was assembled from other collections. Where the nature of the substrate permitted, salamanders were collected by shoveling gravel onto a 6.3 mm mesh wire screen suspended over a large tray. This method is rapid and effective; few if any salamanders fail to move downward through the gravel and into the collecting container. In other sites stones and plant debris were systematically displaced and the salamanders collected with a small net. In general I have found that 50 to 100 salamanders can be collected in less than an hour by either of these methods. Specimens were either preserved in the field, or maintained in the laboratory for periods of up to one year in the course of an investigation of spontaneous and experimentally induced metamorphosis to be reported elsewhere.

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Reproductive and morphological data (except color notes) were taken from preserved specimens. All reproductive data derive from direct examination of the reproductive tracts by dissection. Skeletal characters were examined through a combination of techniques. All specimens were X-rayed, and 22 specimens from transforming populations (16 larval, 6 metamorphosed) were cleared and stained for bone and cartilage using a technique slightly modified from that of Wassersug (1976). The head and neck of one transformed specimen were prepared in serial sections. Series of cleared and stained larval and mature specimens representing all species of Eurycea (except E. junaluska, X-ray examination only), and the remaining genera of hemidactyliine plethodontids were examined, as were sectioned heads of larvae and adults of the majority of species of hemidactyliines. All data and general statements presented here concerning the internal morphology of the head and neck region have been verified by reference to this material.

Detailed distributional information concerning the Texas Eurycea will be presented elsewhere. The material comprising the samples from the six populations of E. neotenes in which metamorphosis is known to occur is listed below. Abbreviations: MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; TNHC, Texas Natural History Collection, University of Texas, Austin; TTU, uncatalogued material loaned by Dr. R. W. Mitchell and Mr. J. R. Reddell, Texas Tech University. Sabinal headwaters, TNHC

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21676 (five specimens), TTU (13 specimens); Wedgeworth Creek, MVZ 119804-119937, 122838-122840; Mill Creek, MVZ 119630-119743, 119937-119952, TNHC 21673 (41 specimens); Sutherland Hollow, MVZ 119386-119488; West Sabinal, TNHC 21669, 21670 (16 specimens); Ash Hollow, MVZ 122142-122364.

Results

Occurrence of Metamorphosing Populations

Populations of E. neotenes are restricted to the vicinity of springs and caves, and are most numerous in the highly dissected headwater region produced by the radial divergence of several major rivers of the Edwards Plateau; the South Fork of the Guadalupe River in southwestern Kerr County, the Medina and Sabinal rivers in western Bandera County, and the Frio River in Real County. Topographic relief diminishes outside of this region, and rainfall decreases to the west, contributing to a relative scarcity of springs suitable for salamander populations elsewhere along the Plateau margin. The distribution of surface populations is indicated by Baker (1961), Brown (1967) and Conant (1975), and more fully outlined by Sweet (1976). Transformed individuals in surface populations of E. neotenes are known only from six localities in this central region of high spring density, chiefly in the drainage of the Sabinal River (Fig. 16). Transformed specimens have been found in the field at sites 2,3,4, and 5, and spontaneous metamorphosis in the laboratory has been noted in

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Figure 16. The range of *Eurycea neotenes* (stippled), and the distribution of metamorphosing populations (insert). Counties are outlined, and the margin of the Edwards Plateau is indicated by the solid line. Metamorphosing populations are represented in the insert by filled circles (numbers as in Table 12); open circles denote exclusively paedogenetic populations.

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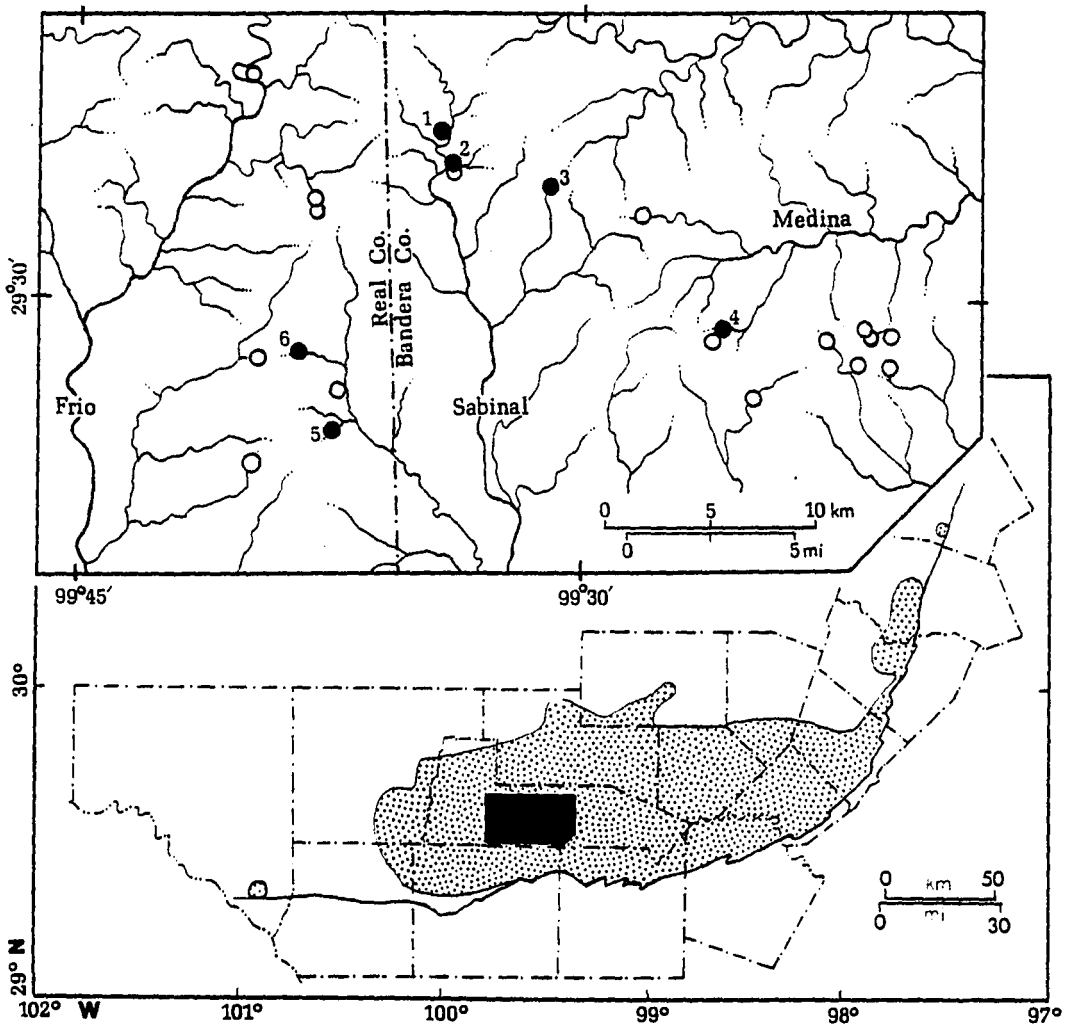

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samples from sites 1, 2, 3, and 6. No metamorphosed individuals occur among 473 specimens from the remaining 16 surface populations indicated in Fig. 16, nor among 94 additional surface populations from throughout the remainder of the range of E. neotenes.

There is some evidence that metamorphosis may occur in two troglobitic populations (presently referred to E. neotenes) in Uvalde County, to the southwest of the Sabinal region. An apparently metamorphosed individual was seen by me but not collected in Carson Cave, southwest of Montell in the Nueces River drainage, and one individual from this population metamorphosed in the laboratory after receiving pituitary implant treatment which was insufficient to induce metamorphosis in other populations (James P. Bogart, personal communication, 1976). A transformed individual was collected in a cave east of Concan, between the Frio and Sabinal drainages (Bryce C. Brown, personal communication, 1970), but was not available for examination.

No evident special features differentiate the Sabinal headwaters (1) and Wedgeworth Creek (2) sites, where transformation is frequent (Table 12), from other localities in the area, nor can a more general distinction between transforming and exclusively paedogenetic populations be made on the basis of habitat characteristics. A subjective evaluation places the canyons of the Sabinal divide as the most mesic region of the Plateau margin, an interpretation suported by the diversity of relict plant species present (Cor-

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Table 12. Location of populations and frequency of metamorphosis of *Eurycea neotenes*. The adult class includes both mature and maturing individuals. Locality numbers correspond to sites indicated in Figure 16.

	Locality	Elevation (m)	Sample size	Adults	
				Paedogenes	Transformed
1	Sabinal Headwaters	561	18	13	4
2	Wedgeworth Creek	564	137	34	27
3	Mill Creek	592	171	108	4
4	Sutherland Hollow	589	101	43	1
5	West Sabinal	494	17	10	1
6	Ash Hollow	561	223	66	1

rell and Johnston, 1970). In this region most populations of E. neotenes occupy narrow headwater canyons (Fig. 17), moderately shaded by spanish oak (Quercus texana), pecan (Carya illinoinensis) and bigtooth maple (Acer grandidentatum), with alternating shallow pools and riffles on bedrock and gravel substrate eroded from basal units of the Edwards Group limestones. Nearly all headwater springs in this area are developed in the relatively porous contact zone between the Glen Rose Formation and the overlying basal Edwards Group, consisting of the Fort Terrett Formation or the laterally equivalent Devils River Formation (Rose, 1972). A few springs occur along the edges of larger streams in faults in the Glen Rose. Water temperatures of 18° to 21°C are characteristic of all sites, with little annual fluctuation (Brune, 1975).

Transformed and paedogenetic individuals alike are found in gravel and submerged leaf litter, or resting exposed in pools; no transformed animals have been found on shore, although seemingly suitable microhabitats exist in such places as narrow strips of gravel, cobble and flood debris. This habitat may be utilized by transformed salamanders, perhaps at night or during rains, as examined stomachs contain only riparian collembolans and isopods, which are not represented in the guts of larvae.

Population Structure and Reproductive Condition

Table 12 summarizes the frequency of transformed and

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Figure 17. Headwaters of Mill Creek, Bandera County, Texas. This relatively large spring with extensive rocky borders supports a large population of *Eurycea neotenes*, including a few naturally metamorphosed individuals. Photograph taken 22 August 1971.

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paedogenetic adult salamanders in the six metamorphosing populations; the adult category combines mature and maturing individuals as characterized by Bruce (1976). Females with thin, straight oviducts and ova in early stages of vitellogenesis, and males with single testis lobes and nonconvoluted vasa deferentia were designated by Bruce (1976) as maturing. Females with thickened oviducts and a mixture of clear and vitellogenic ova, and males with 1 lobe per testis and pigmented, convoluted vasa deferentia were considered mature. All maturing and mature individuals were 25 mm in standard length (tip of snout to posterior margin of cloaca) or larger.

Transformed salamanders comprise a significant proportion of the adult population in the Sabinal headwaters and Wedgeworth Creek sites. There is evidence from both material collected in the field and samples maintained in the laboratory that in these populations most if not all individuals surviving to maturity transform. The size frequency distribution of specimens from three collections made in July at the Wedgeworth Creek site (Fig. 18) indicates considerable overlap between larval and transformed individuals; however, the two groups are distinct in reproductive condition. None of the larval specimens is mature, whereas eight of the 11 transformed specimens are mature. All specimens >30 mm in standard length are immature. The largest larval specimen (34.7 mm) is a male with single lightly pigmented testis lobes 4.5 mm in length and straight, unpigmented vasa

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Figure 18. Size frequency distribution of standard lengths of 99 *Eurycea neotenes* from Wedgeworth Creek, Bandera County, Texas. The figure combines collections made on 23 July 1973 (30 specimens), 13 July 1974 (67 specimens) and 18 July 1974 (2 specimens).

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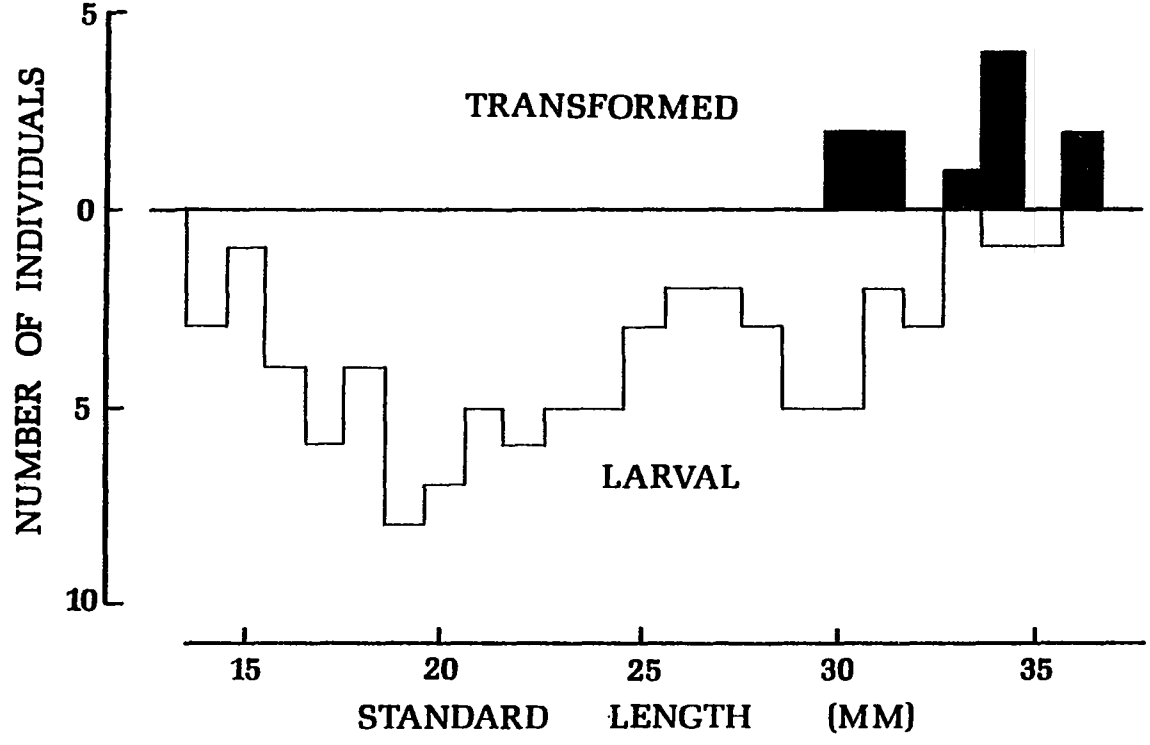

deferentia. Three other larval males >30 mm in standard length have small (0.5-1.2 mm) lightly pigmented posterior expansions of the testis cord and straight, unpigmented vasa deferentia. The eight larval females >30 mm in standard length have thin, straight oviducts and tiny (~0.5 mm) clear ova, as does the smallest (30.6 mm) transformed female. Three of the four remaining transformed females in this sample (33.7, 34.5 and 36.0 mm) are vitellogenic, with a mixture of tiny clear ova and small (0.6-1.0 mm) yolking ova; the oviducts of these females are wide but straight. The remaining transformed female (35.7 mm) has expanded and moderately convoluted oviducts, and large (1.0-2.0 mm) yolked ova on one side, with a large yolky mass apparently undergoing resorption contralaterally. The two smallest transformed males (both 30.0 mm) in this sample have single lobed, heavily pigmented testes, and lightly pigmented, straight vasa deferentia. The remaining four transformed males have convoluted and heavily pigmented vasa deferentia; two (31.0, 32.7 mm) have 1,2 testis lobes, one (34.0 mm) has 2,2 lobes, and one (34.0 mm) has 2,3 lobes.

Forty specimens from this locality were maintained in the laboratory for about six months (September 1973 to March 1974); during this time six of 10 control individuals ≥25 mm in standard length metamorphosed without treatment. These specimens, consisting of three males and three females between 30.0 and 32.0 mm in standard length, were preserved soon after transformation; all are in the process of matura-

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tion, the males showing single testis lobes and pigmented, straight vasa deferentia, and the females having tiny clear ova and thin, straight oviducts.

Part of the sample from the Sabinal headwaters population was maintained in the laboratory, where at least one specimen of the series metamorphosed without treatment (Bogart, 1967). The transformed specimens are mature (two males, 2,2 testis lobes; two females with small vitellogenic ova) in contrast to the larval specimens, which are immature or in a stage of maturation comparable to that of larvae from the Wedgeworth Creek population.

The evidence presented here indicates that when metamorphosis occurs it is contemporaneous with the attainment of sexual maturity. There is no evidence for the metamorphosis of individuals which have previously matured as paedogenes. Larval specimens comprise two size classes in the Wedgeworth Creek population (Fig. 18); those in the larger size class are approaching maturity, suggesting that maturation occurs in the second year of life in this population, as was demonstrated by Bruce (1976) for two populations of E. neotenes from the Guadalupe River drainage.

The situation in the Wedgeworth Creek and Sabinal headwaters populations is in contrast to that observed in the four other populations in which transformed individuals are known. In each of these localities transformed salamanders are uncommon (Table 12). Despite the large number of specimens collected (in July, August and September), mature in-

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dividuals are few in the Mill Creek, Sutherland Hollow and Ash Hollow samples. Only two larval females from Mill Creek have vitellogenic ova and enlarged oviducts; other females ≥ 25 mm in standard length have tiny clear ova and thin straight oviducts. The single transformed specimen found in the field at this site is a 34.0 mm male, with large testes composed of small posterior and large (4.0 mm) anterior lobes; the vasa deferentia are heavily pigmented and convoluted. While most larval males ≥25 mm in this sample have single testis lobes 3-4 mm in length, none has coiled or heavily pigmented vasa deferentia.

One larval male from Sutherland Hollow (32.3 mm) is mature, with 2,3 testis lobes and convoluted and heavily pigmented vasa deferentia; the remaining larval males and females ≥ 25 mm are maturing. The transformed specimen from this population is a 34.5 mm female, with 0.5-0.7 mm vitellogenic ova and expanded oviducts.

None of the larval specimens from the Ash Hollow population is mature, though all individuals ≥ 25 mm are in the process of maturation. A single male (32.5 mm) which metamorphosed without treatment in the laboratory has enlarged testes and convoluted vasa deferentia comparable to the reproductive tract of the Mill Creek male.

Six of the 10 larval specimens ≥ 25 mm in standard length from the West Sabinal population are sexually mature. Two males (both 33.4 mm) have 2,2 testis lobes and enlarged, tightly convoluted vasa deferentia. Two females (28.3, 28.7

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mm) each contain nine large (3-4 mm) ova apparently ready for deposition, in addition to 7-10 smaller (0.7-1.0 mm vitellogenic ova. In one of these females an egg lies free of the ovary in proximity to the ostium of the oviduct; two ovarian eggs remain on this side, with six contralaterally. A third female (29.6 mm) in this January sample contains no yolked ova, but has enlarged oviducts, suggesting that egg deposition had recently occurred. The remaining mature larval female (28.2 mm) contains numerous 1.0-2.0 mm ova, and has expanded oviducts. The transformed female (33.5 mm) from this population has large (3.0-4.0 mm) ova and enlarged, convoluted oviducts.

In summary, paedogenetic and mature transformed specimens are known from the Sutherland Hollow and West Sabinal populations; only transformed individuals are mature in the Sabinal headwater, Wedgeworth Creek, Mill Creek and Ash Hollow samples. All but one are summer collections, and since the evidence from the West Sabinal population suggests that reproduction occurs in midwinter, it is possible that some larval individuals may mature during the fall without metamorphosing. Further samples will be necessary to determine the degree of variability in the composition of breeding populations in these sites.

Morphology of Transformed Specimens

Transformed specimens of E. neotenes (Fig. 19) are gracile, and differ from other species of Eurycea in being

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Figure 19. Naturally transformed (lower) and larval specimen (upper) of *Eurycea neotenes* from Wedgeworth Creek population. Note the scattered dorsal iridophores and uniform ground color of the metamorphosed individual, and its somewhat stouter limbs. Scale bar = 20 mm.

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uniformly dark dorsally, without traces of the spots, chevrons or bands characteristic of other species. In this respect E. neotenes most closely resembles some populations of E. multiplicata of the Interior Highlands. The dorsal ground color of E. neotenes in life is dark brown (Bone Brown, Ridgway [1912]), with scattered silvery iridophores present on the dorsal trunk, increasing in density laterally on the trunk and tail. The melanophores of the dorsal surface remain equally dense passing laterally on the tail, but are abruptly diminished ventral to the boundary of the epaxial musculature on the trunk, and ventral to the postocular groove on the head (Fig. 19); the combination of reduced melanophores and increased iridophores produces a grayish, salt-and-pepper effect laterally. There are numerous scattered melanophores on the venter, which is translucent white; liver, spleen, intestine, gonads and fat bodies are clearly visible. Fat deposits impart a yellow tone to the ventral midline of the tail. The iris is brassy with a brown periphery.

All transformed specimens show a strip of dark pigment in the connective tissues internal to the epibrachial sheath in the region of the gular fold, which derives from the epithelia of the degenerating gill rami at metamorphosis. This strip becomes less evident during the first three months following metamorphosis, but apparently persists throughout life in E. neotenes as it does in other species of Eurycea, and in Gyrinophilus, Pseudotriton and Stereochilus; it is

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thus not a reliable indicator of recent metamorphosis.

Transformed specimens range from 30-36 mm in standard length. The head (Fig. 20) is slender with large protruberant eyes; eyelids are fully formed and functional, with the transverse posterior fold characteristic of fully metamorphosed salamanders. Neither cirri nor externally apparent mental glands are developed in the available males. A nasolabial groove is present, and the origins of the gular musculature produce a sinuous groove extending from the posterior margin of the eyelid to the gular fold. The epibranchial sheath extends laterally beyond the gular fold to a point anterior to the forelimb insertion. Seventeen (rarely 18) trunk vertebrae are present, and 16 or 17 costal grooves; adpressed toe tips are separated by four or five costal folds. The tail is slender, comprising slightly less than half of the total length, with from 32-40 caudal vertebrae; it is oval at the base becoming laterally compressed distally. A dorsal glandular complex is present on the tail base of the Mill Creek male estimated to be >2 years of age on the basis of bilobed testes.

The skull (Fig. 21a,b) is lightly constructed and fully metamorphosed, corresponding in most respects to the skulls of other transformed Eurycea as characterized by Wake (1966). The premaxilla is single, and the facial lobe of the maxilla arises from the middle third of that element. There are 10-16 premaxillary teeth, 32-46 maxillary teeth, 13-18 teeth in the anterior vomerine series, and 46-62

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Figure 20. Dorsolateral view of the head of MVZ 119886, a 35.7 mm mature *Eurycea neotenes* female from the Wedgeworth Creek population.

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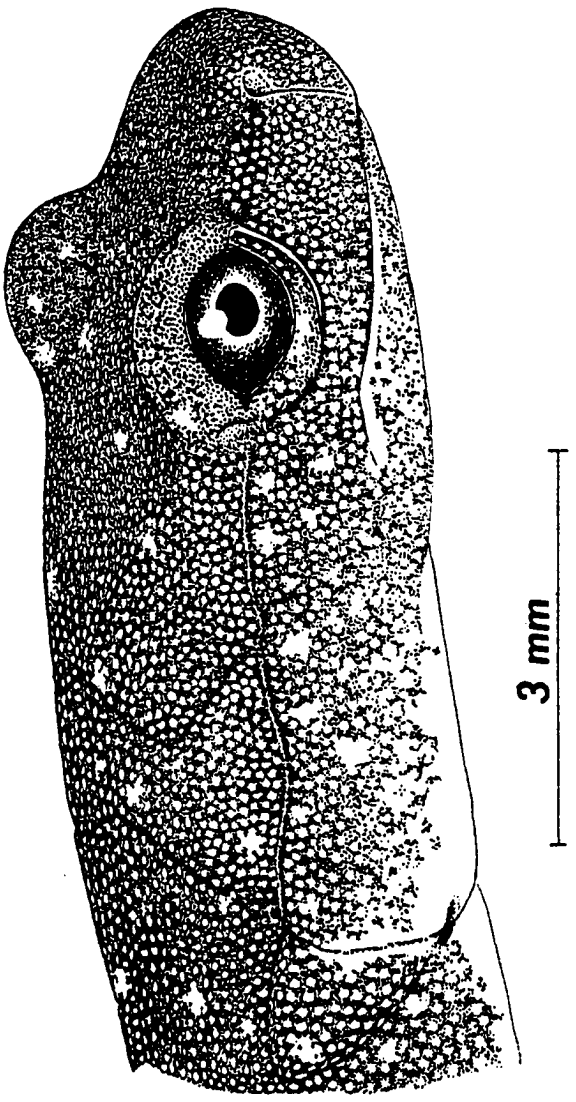

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Figure 21. Dorsal (a) and ventral (b) views of the skull and dorsal aspect of the hyobranchial apparatus (c) of MVZ 119884, a 32.0 mm mature *Eurycea neotenes* male from the Wedgeworth Creek population. Cartilage is stippled.

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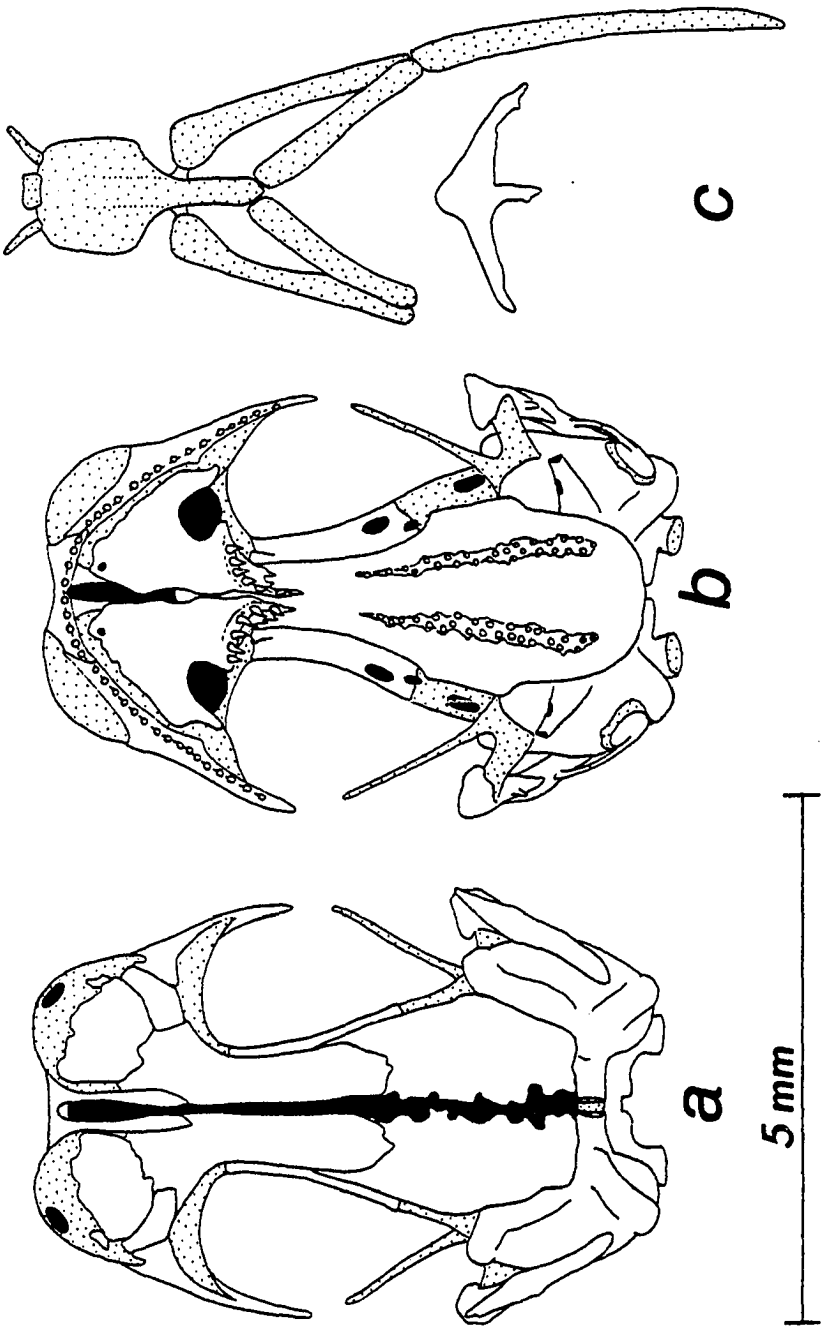

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teeth in the posterior vomerine series; dentary teeth number 40-51 (all counts combine left and right sides). No ontogenetic increase in premaxillary or vomerine teeth has been noted; larger individuals tend to add teeth at the posterior ends of the maxillary and dentary series. Premaxillary and anterior maxillary teeth are enlarged in the Mill Creek male. The preorbital process of the vomer is short, not extending beyond the margin of the internal nares in older individuals. At metamorphosis the larval vomer degenerates posteriorly, its anterior portion becoming the body of the preorbital process of the adult vomer (Wilder, 1925); for a short time during metamorphosis the preorbital process is long and posterolaterally oriented as in primitive hemidactyliine genera (Wake, 1966), becoming shortened and laterally directed as the adult vomer takes form. The posterior vomerine (parasphenoid) tooth series develops in continuity with those of the vomer in E. neotenes as in all other hemidactyliines; a discontinuity arises after metamorphosis in most species of Eurycea (Wake, 1966), including E. neotenes, by the loss of the anterior teeth in the parasphenoid series. The orbitosphenoid is ossified from the preorbital process to a point posterior to the optic foramen at metamorphosis, with age extending posteriorly to partially enclose the oculomotor foramen. The bony crests developed on the otic, parietal and squamosal bones of some species of Eurycea (E. aquatica, E. bislineata and E. junaluska) are lacking in available material of E. neotenes. The

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cartilaginous portions of the suspensorium are comparable to those of other species of Eurycea. An opercularis slip of the scapular musculature is present.

Two features of the anterior margin of the orbit are unique within the genus to transformed E. neotenes (Fig. 22); (1) the nasolacrimal foramen characteristic of Eurycea (Wake, 1966) is absent; and (2) the prefrontal generally separates the nasal from contact with the facial lobe of the maxilla (10 of 13 cases examined). The nasolacrimal duct of Eurycea other than E. neotenes passes across the body of the prefrontal and through a foramen developed at the contact of the prefrontal and nasal, passing internal to the lateral process of the nasal to join the nasal capsule at the posterior margin of the septomaxilla (Wilder, 1925; Lapage, 1928; Wake, 1966). The duct arises at metamorphosis prior to the ossification of the nasal and prefrontal and molds the contact zone of these elements in a characteristic fashion. The foramen is generally large and distinct in Eurycea (Fig. 22), but tends to be irregular in shape in E. multiplicata, and is occasionally absent unilaterally. Eurycea neotenes resembles the primitive hemidactyliine genera Gyrinophilus, Stereochilus and Typhlotriton in that the course of the nasolacrimal duct is external to the nasal, without the deep groove on the prefrontal characteristic of Pseudotriton (Joubert, 1961; Wake, 1966).

In most transforming species of Eurycea (except E. quadridigitata and E. neotenes)the prefrontal is extensive-

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Figure 22. Left lateral aspect of the anterior margin of the orbit in Eurycea and Typhlotriton; (a) the general condition in Eurycea (E. aquatica, E. bislineata, E. junaluska, E. longicauda, E. guttolineata, E. lucifuga, and some E. multiplicata); (b) E. quadridigitata; (c) E. neotenes; (d) Typhlotriton spelaeus. Abbreviations: s, septomaxilla; n, nasal; f, frontal; p, prefrontal; m, facial lobe of maxilla; nlf, nasolacrimal foramen. Overlapped regions of the prefrontal are stippled.

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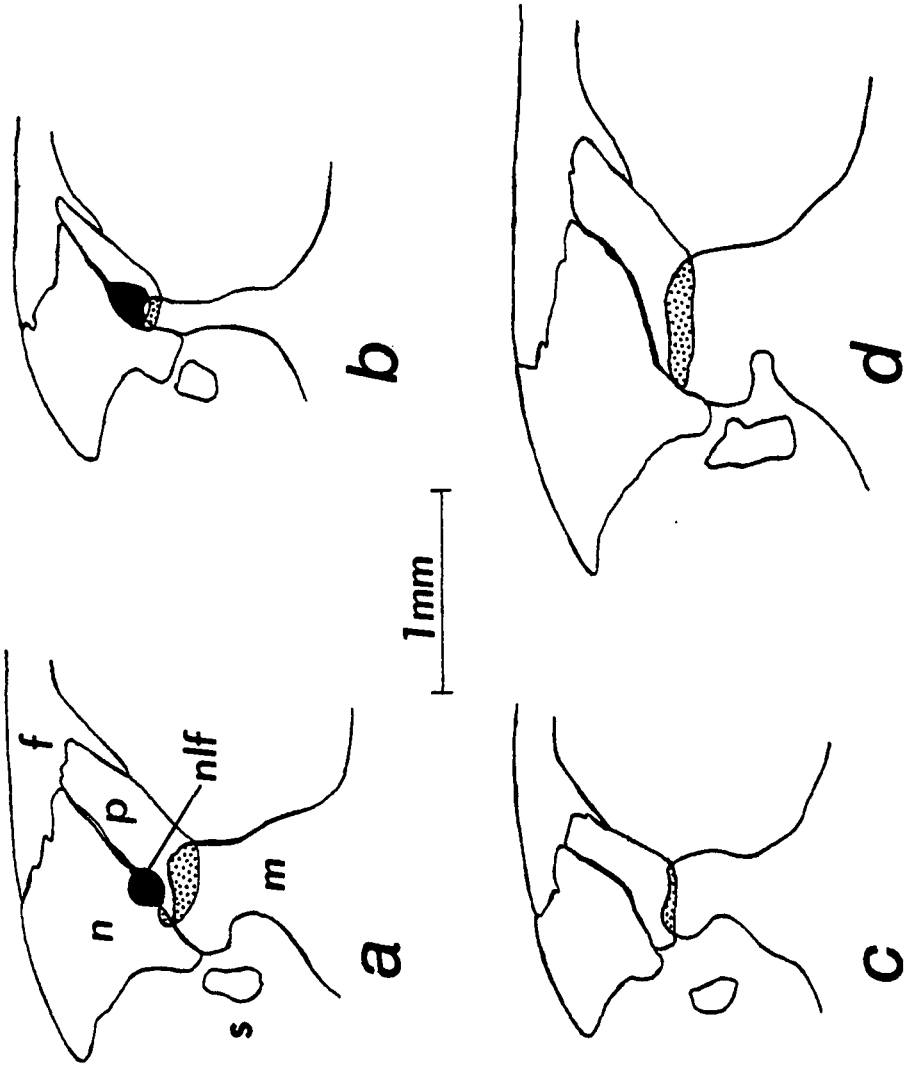

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ly overlapped by the maxilla and nasal as ontogeny proceeds, these elements coming into contact anterior to the nasolacrimal foramen (Fig. 22). The prefrontal of E. neotenes is large, and permits little or no anterior overlap in most specimens examined. Three specimens show fusions of the bony elements in the antorbital region; prefrontals and nasals are fused in one specimen from Wedgeworth Creek, as are the prefrontals and maxillae in both examined specimens from the Sabinal headwaters populations.

The hyobranchial apparatus (Fig. 21c) is fully metamorphosed and functional; transformed individuals feed readily on Drosophila in the laboratory. The basibranchial is greatly expanded anteriorly, and bears short but well-developed radii; a lingual cartilage is present. The epibranchials represent ~45% of the total length of the apparatus. The urohyal is large and ossified, and is approximately equal in width to the length of the basibranchial. These features of the hyobranchial skeleton, and its musculature (examined in sectioned material) are consistent with Mode IV of Lombard and Wake (1977), which includes the genera Eurycea and Typhlotriton. Unlike the latter genus, the tongue pad of transformed E. neotenes is free anteriorly, without the connective tissue strip and remnants of genioglossus musculature characteristic of Typhlotriton (Piatt, 1935b; Lombard and Wake, 1977).

The postcranial skeletons of transformed and paedogenetic E. neotenes are similar; the feet are slightly larger

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in transformed individuals. Vertebral proportions fall within the range of Eurycea and Typhlotriton as characterized by Wake (1966); transverse processes are short, with the parapophyses entirely anterior to the diapophyses. Hyperapophyses are discrete and pointed, extending beyond the postzygapophyses of trunk and anterior caudal vertebrae. Basapophyses are variably developed in the Texas Eurycea; in transformed E. neotenes they are small, and developed only in the midtrunk region.

Discussion

Generic Allocation of Texas Eurycea

Features diagnostic of the genera Eurycea and Typhlotriton are primarily those of the hyobranchial apparatus and vertebrae (Wake, 1966); the two genera are distinguished by the attached tongue, external route of the nasolacrimal duct, a tendency for division of the premaxilla, long preorbital processes and divergent, continuous vomerine tooth series of Typhlotriton. Transformed E. neotenes conform to the hyobranchial and vertebral features of this pair of genera in every respect; they share with other members of the genus Eurycea the characters of: tongue free anteriorly; single premaxilla; short preorbital processes; and discontinuous vomerine tooth series, with the posterior patch medially situated. The external route of the nasolacrimal duct is shared with Typhlotriton, but is approached by the condition seen in E. multiplicata. The weight of evidence

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indicates that E. neotenes is correctly assigned to the genus Eurycea.

Eurycea neotenes seems most closely related to E. multiplitcata and E. tynerensis of the Interior Highlands, sharing with them the following attributes: often or usually paedogenetic; light dorsal stripe, cirri, and nasolacrimal foramen reduced or absent in metamorphosed individuals; 17 or more trunk vertebrae in surface populations; tail rounded in section at base; dorsal glandular complex on tail base of metamorphosed males; and testes lobed. In contrast to the report of Sever (1974), most of the adult males of E. tynerensis and E. multiplicata which I have examined have bilobed testes.

Evaluation of the generic allocation of other populations in the central Texas paedogenetic assemblage must be made on the basis of larval features by comparing the morphology of E. neotenes to the range of diversity displayed by numerous surface and troglobitic populations. The known cave populations generally assigned to Eurycea (E. latitans and E. troglodytes Reddell, 1967, 1971; Mitchell and Smith, 1972) are closely allied to the surface populations from which they derive. A detailed analysis of this group is in preparation; at present there is no evidence of structual heterogeneity which would suggest that the surface and intermediate cave forms are not congeneric. The questions posed by the morphological similarities among populations of the advanced troglobite E. tridentifera (Sweet, 1977) and

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Typhlomolge rathbuni (Russell,1976) are more complex. Wake (1966) removed E. tridentifera to Typhlomolge on osteological grounds, but Mitchell and Reddell (1965) and Mitchell and Smith (1972) have argued for the inclusion of T. rathbuni in Eurycea. The status of the genus Typhlomolge and the allocation of E. tridentifera is the subject of another investigation.

Metamorphosis and the Origin of Paedogenesis

Bruce (1976) proposed a model for the origin of paedogenesis in the Texas Eurycea which is strongly dependent on two factors: (1) the existence of an environmentally-determined minimum size limit on metamorphosed salamanders; and (2) high juvenile mortality, on the order of 80-90% during the first year of life. Bruce suggested that selection for reduced age at first reproduction results in adults which are below the size limit for ecologically feasible metamorphosis into the arid terrestrial zone. Both assumptions of this model are qualified by evidence presented here. Transformed individuals of E. neotenes have been found to be predominantly aquatic in the field and in the laboratory, though they apparently feed terrestrially; in the laboratory all salamanders observed feeding were at least partially out of water. They appear to avoid the rigors of the terrestrial environment in large part. The presence of large fat bodies and mature gonads in metamorphosed specimens argues against the existence of strong selective disadvantages to

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metamorphosis in these populations.

Bruce (1976) based his finding of high juvenile mortality on samples collected during a two-week period from two populations, Fall Creek and Lambs Creek, both in southern Kerr County. In samples of 215 and 393 individuals, respectively, Bruce found 10% and 18% to be adult (maturing and mature categories combined). My samples from these populations uniformly contain a higher percentage of adults (here considered to be those individuals ≥25 mm in standard length); the figures are: Fall Creek: 1973, n=113, 26% adult; 1974, n=112, 25% adult. Lambs Creek: 1971, n=34, 62% adult; 1973, n=26, 61% adult; 1974, n=125, 57% adult. Samples of 50 or more individuals from 20 other populations range from 18-71% adult ($\bar{x}$=53%). These data may reflect differences in our collecting techniques; however, the observed local variation in apparent population composition illustrates the need for caution in generalizing population strategies from few sites. As a further caution, I have noted that apparent population structure varies with the amount of spring flow; drying conditions generally result in a disproportionate reduction in the number of small salamanders on the surface, though often only these juveniles remain as a spring becomes essentially dry and the remaining adults disappear. Thus, while the general conclusion of high juvenile mortality is probably valid, the magnitude of this effect remains to be satisfactorily determined.

I suggest that while the origin of paedogenesis in the

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Texas Eurycea is clearly related to the limitation of suitable habitat, the probable causal factors differ from those which have been previously proposed. Metamorphosis remains a feasible life history strategy in some populations of the Sabinal divide region, where relatively mesic conditions prevail. This may be due in large part to the relative stability in groundwater levels characteristic of the area, which owes to the broad adjacent recharge surface of the undissected uplands of the Plateau. Springs in this region appear to be temporally reliable, and thus provide stable aquatic habitats above the ground surface. I have observed that in other areas distant from the high Plateau, many springs with populations of Eurycea neotenes undergo episodic fluctuations in discharge, some becoming dry for periods of weeks or months; during this time the resident salamander population is obliged to retreat underground via the spring channels. The selective disadvantages of metamorphosis may be most pronounced under conditions of unreliable spring flow; in this situation paedogenetic individuals may continue to feed while underground, but the adaptations for terrestrial feeding in transformed individuals are much less effective underwater and in darkness. The persistence of metamorphosis in populations of the Sabinal divide region probably reflects the consistent availability of surface water; paedogenesis seems to be a response to selection for the ability to pass dry periods in subterranean aquatic refugia.

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CHAPTER VI

SECONDARY CONTACT BETWEEN EPIGEAN AND TROGLOBITIC POPULATIONS OF THE TEXAS *EURYCEA*

Introduction

Populations of the small aquatic salamanders of the genus *Eurycea* on the Edwards Plateau of central Texas are diverse and distinctive. Prominent is a graded series of cave-adapted forms that range from those of essentially unmodified epigean morphology to populations in an advanced troglobitic state characterized by depigmentation, extreme eye reduction, and hypertrophy of locomotor and feeding structures (Mitchell and Smith, 1972). Most of the populations constituting this adaptive trend are morphologically homogeneous, and display a high degree of concordance in the set of characters showing directional change. As currently understood, many of these populations represent independent lineages evolving in parallel (Sweet, 1977a); nearly all are allopatric. However, salamanders from three of 21 cave localities show unusually high levels of variability and character discordance that may reflect hybridization between individuals from surface and advanced cave populations. At one cave epigean and troglobitic populations are demonstrably sympatric and undergo limited hybridization; certain characteristics of the other two populations suggest that they are hybrid swarms.

Structural intermediacy, increased levels of individual

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variability and discordance in character states within individuals with respect to parental populations together constitute primary morphological evidence for the occurrence of hybridization. Genetic evidence from electrophoretic analyses also has potential value in demonstrating hybridization if the parental populations can be differentiated. A survey of available material (Yanev and Sweet, unpublished) indicates that there are few, if any, unique alleles among a diversity of populations of the Texas Eurycea. Frequency differences may exist, but small sample sizes compromise the use of this evidence and of individual heterozygosity values. As a result, the following analysis is based on morphology alone. I will show that the morphological criteria noted above are fully met in two instances, and partially so in the third. Further, the composition of one of the two suspected hybrid swarms has apparently shifted in recent years towards a lesser degree of troglobitic specialization. The degree to which hybridization occurs seems to be inversely related both to the inferred frequency of contact between the parental populations, and to the relative amount of environmental heterogeneity in the locations where contact takes place. In one cave in which the populations remain largely distinct there is a possibility of competitive exclusion of the epigean population by its specialized troglobitic counterpart.

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Materials and Methods

Primary data in this paper were derived from the following preserved materials. Honey Creek Cave, 7.7 km SW Spring Branch, Comal County: 59 E. tridentifera, 6 E. neotenes, and 4 intermediate individuals; Valdina Farms Sinkhole, 34 km NW Hondo, Medina County: 41 E. troglodytes; and Cascade Caverns system, 5.3 km SE Boerne, Kendall County: 17 E. latitans. These sites, and other known localities for E. tridentifera are shown in Figure 23. For comparison with E. troglodytes I have used 53 specimens of E. neotenes from the Seco Creek drainage upstream from Valdina Farms Sinkhole, and 46 E. tridentifera from Badweather Pit, Comal County, the closest known population of this suspected parental taxon. The Badweather Pit sample and 50 E. neotenes from the headwaters of Cibolo Creek were used as reference samples in comparison with E. latitans. Data from several other samples of surface and troglobitic Eurycea are presented for comparative purposes where appropriate. Particularly useful is a series of 34 specimens of an undescribed species (Sweet, in preparation) from the eastern margin of the Edwards Plateau in Travis County; this population is referred to herein as E. sp.. Individuals from this population resemble "averaged" specimens of E. troglodytes or E. latitans, yet show a normal pattern of variability among individuals. As such they indicate that the unusual characteristics of these taxa are not necessary correlates of an intermediate level of troglobitic specialization.

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Figure 23. Map of the southeastern margin of the Edwards Plateau, illustrating the distribution of several troglobitic populations of *Eurycea* with respect to the Balcones Fault Zone and the Cibolo sinkhole plain (stippled area). Numbered localities are as follows: 1, Valdina Farms Sinkhole (*E. troglodytes*); 2, Cascade Caverns and Cascade Sinkhole (*E. latitans*); 3-8, *E. tridentifera*: 3, Badweather Pit; 4, Grosser's Sinkhole; 5, Calmbach Cave; 6, Honey Creek Cave (*E. tridentifera* in sympatry with *E. neotenes*); 7, Kappelman Salamander Cave; 8, Elm Springs Cave. Fault structure adapted from Rose (1972) and San Antonio Sheet, Geologic Atlas of Texas (1974).

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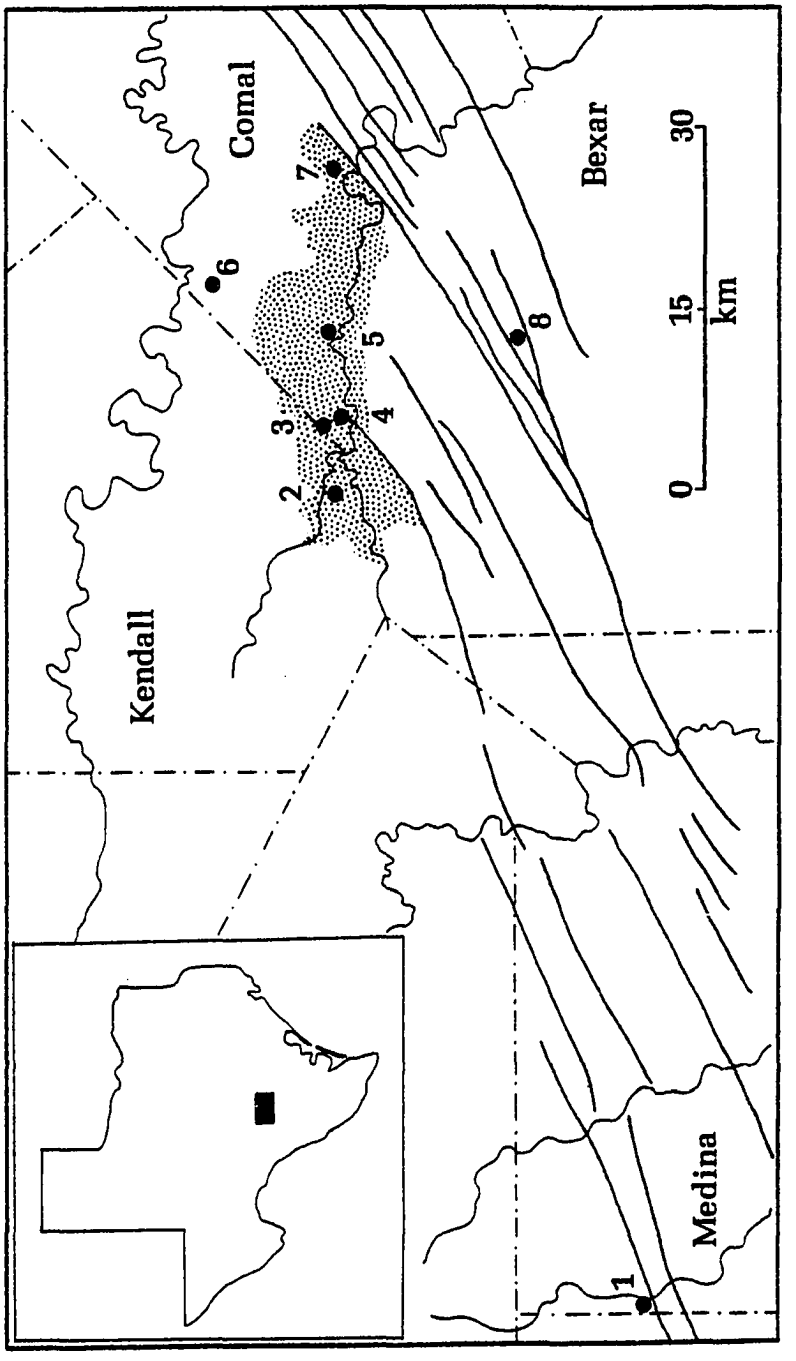

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Several population samples of Eurycea neotenes from caves and springs of the Guadalupe canyon in Comal and Kendall counties are employed in an analysis of the possible effects of competitive exclusion at Honey Creek Cave. These samples (site name, site number as shown on Fig. 31 , location, sample size) are: Behr's Cave, 1, 16.5 km N Boerne, Kendall County, 4 specimens; Victor Phillip Water Cave, 2, 11.0 km NNE Boerne, Kendall County, 21 specimens; Golden Fawn Cave, 3, 11.8 km NNE Boerne, Kendall County, 1 specimen; Alzafar Water Cave, 4, 13.3 km NE Boerne, Kendall County, 14 specimens; Deadman's Cave, 5, 16.0 km NE Boerne, Kendall County, 15 specimens; Honey Creek cave, 11, 6 specimens; Bender's Cave, 13, 4.5 km NW Spring Branch, Comal County, 38 specimens; Puter Creek Spring, 15, 5.6 km NE Spring Branch, Comal County, 49 specimens; and Rebecca Creek Spring, 16, 6.2 km NE Spring Branch, Comal County, 3 specimens.

Most of the specimens reported here are housed in the Museum of Vertebrate Zoology, University of California, Berkeley; a complete listing of collection numbers and localities for all Texas Eurycea is presented in Appendices I, II and IV.

The following measurements and counts were selected for analysis: standard length (SL)- tip of snout to posterior margin of cloaca; head length a (HLA)- tip of snout to gular fold at midventral line; head length b (HLB)- tip of snout to dorsal margin of third gill ramus; head length c (HLC)- posterior margin of eye to third gill ramus; head width (HW)-

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span at jaw articulation; eye diameter (ED)- silhouette of optic cup in transverse plane; interorbital distance (IOD)- span between silhouettes of optic cups; axila-groin (AG)- posterior margin of forelimb to anterior margin of hind limb; hind limb length (HLL)- groin to tip of third digit; number of trunk vertebrae (TV)- atlas and sacrum excluded; premaxillary (PM), vomerine (VO), palatopterygoid (PAL) and dentary (DT) teeth - number of tooth pedicels on each element, rather than number of seated teeth, left and right sides combined. All measurements were made to the nearest 0.1 mm using dial calipers (SL) or an ocular micrometer. Vertebral and tooth counts were made from either cleared and stained specimens or high resolution X-ray negatives.

The data were analyzed with the aid of the University of California, Berkeley CDC 6400 computer, using the SPSS programs for correlation and discriminant analyses. Values for Kendall's coefficient of concordance (Siegel, 1956) were calculated manually. Specimens with incomplete data were excluded; sample sizes and characters employed vary accordingly and are specified for each series of tests.

Results

Cases of Secondary Contact

Honey Creek Cave

Honey Creek Cave (Reddell, 1964) is one of a number of small stream caves opening into the canyon of the Guadalupe River and its tributaries in Kendall and western Comal Coun-

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ties. The river has developed incised meanders in this area, transecting tributaries of one or more regional subterranean drainage systems which are now enlarging as isolated local drainages. Most of these caves discharge as springs and a thorough survey has shown that most are inhabited by Eurycea. An apparently disjunct population (Sweet, 1977b) of the advanced troglobite E. tridentifera occupies the Honey Creek Cave drainage, as does a population of the widespread surface species E. neotenes (Mitchell and Reddell, 1965). The outflow of this cave is short and steep, and salamanders are not easily collected; repeated efforts have yielded only 6 E. neotenes in contrast to over 60 E. tridentifera, which are easily collected in the still waters of the cave. No E. tridentifera has been found outside of the cave, and despite careful search only one E. neotenes has been found within (Mitchell and Reddell, 1965; specimen figured by Bogart, 1967, plate 6a). Four salamanders have been found within the cave which appear to be hybrids on the basis of structural intermediacy. Representatives of E. neotenes, E. tridentifera, and a presumed hybrid are shown in Figure 24.

Valdina Farms Sinkhole

The continuous aquatic transition from surface to cave environments at Honey Creek Cave and other sites in the Guadalupe canyon is absent at Valdina Farms Sinkhole. This large cave (mapped and described in Reddell, 1967a) consists of a 50 m deep collapse sink intersecting a long roughly horizon-

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Figure 24. Representative *Eurycea* from Honey Creek Cave, Comal County, Texas. The epigean *E. neotenes* (MVZ 120383) shown on the left may hybridize with the advanced troglobite *E. tridentifera* (MVZ 120544) shown on the right. The center pair of specimens (MVZ 120390, 120391) are believed to be hybrid individuals. The scale bar = 10 mm.

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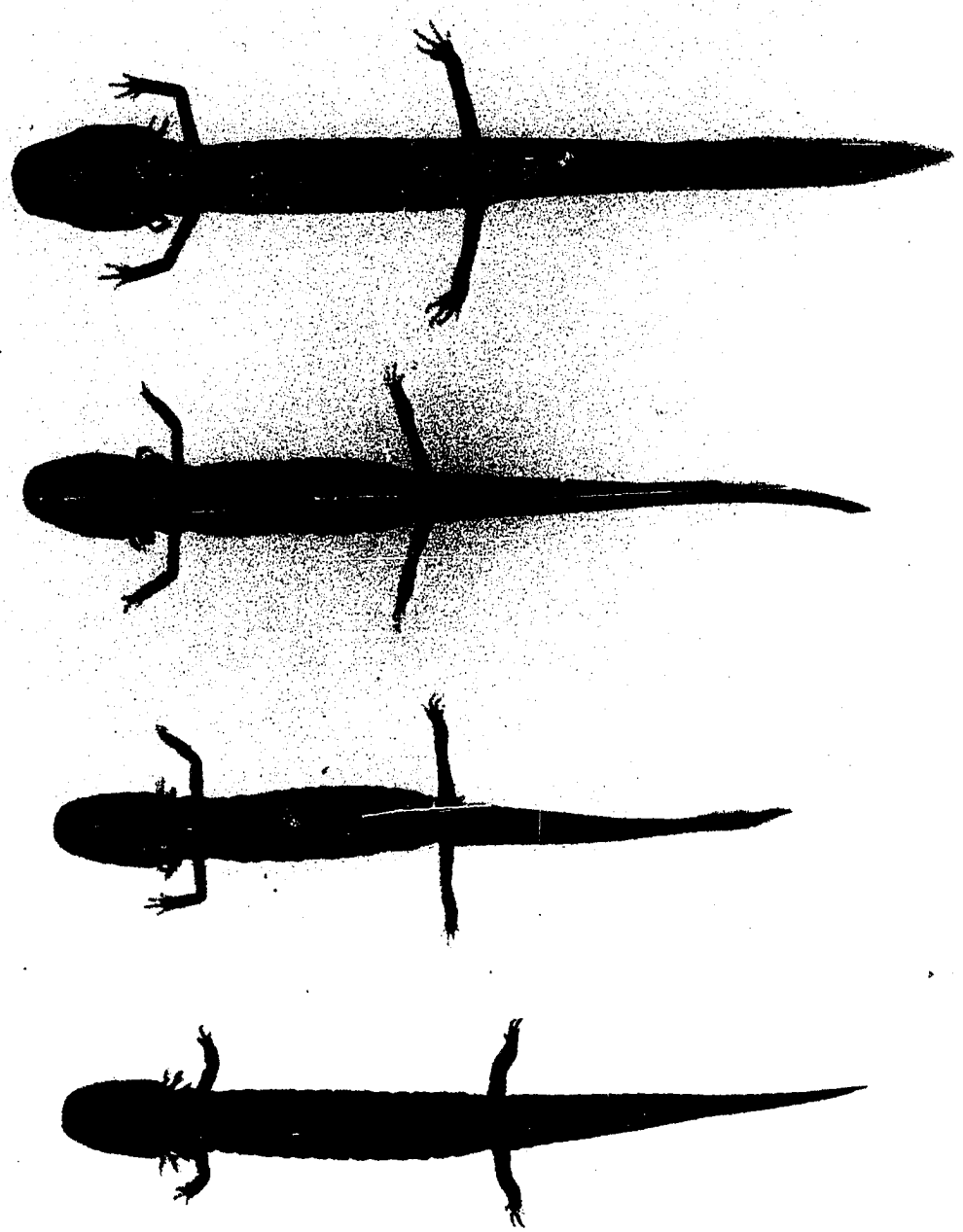

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tal passage that dips into a stream in several sections. This stream has no local discharge point, flowing at a level ranging from 30-60 m below the minimum elevation of the land surface for many kilometers around. The accessible cave passages are adjacent and parallel to the Woodward Fault, a major component of the Balcones Fault Zone having a surface expression of about 60 km (Geol. Atlas of Texas, San Antonio Sheet, 1974). The passages of Valdina Farms Sinkhole are probably in continuity with the network of large solutional openings along this fault and with similar regional channels which together comprise the Edwards Aquifer (Pettit and George, 1956; Garza, 1966). Discharge from this aquifer occurs at large springs along the Balcones Escarpment, the nearest of which is located about 85 km SE of Valdina Farms Sinkhole.

Eurycea troglodytes was described from Valdina Farms Sinkhole on the basis of 20 specimens collected in 1957 (Baker, 1957). Since that time an additional 25 specimens have been collected, most in 1967 (7) and in 1972, 1973, and 1974 (14). This population differs strikingly from other Texas Eurycea in displaying considerable individual variability in coloration and morphology; Figure 25 illustrates a series from the 1974 collection typifying the observed range. Bogart (1967, plate 6b) figures similar extremes from the 1967 collection. Baker (1957) noted the existence of considerable variation in the type series in coloration, eye size and limb proportions. This observation extends to a number of other characters as discussed below.

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Figure 25. A series of *Eurycea troglodytes* from the 1974 collection from Valdina Farms Sinkhole, Medina County, Texas (MVZ 122141-122135) showing the extreme range and intermediate conditions present in this population in coloration and body proportions. The scale bar = 10 mm.

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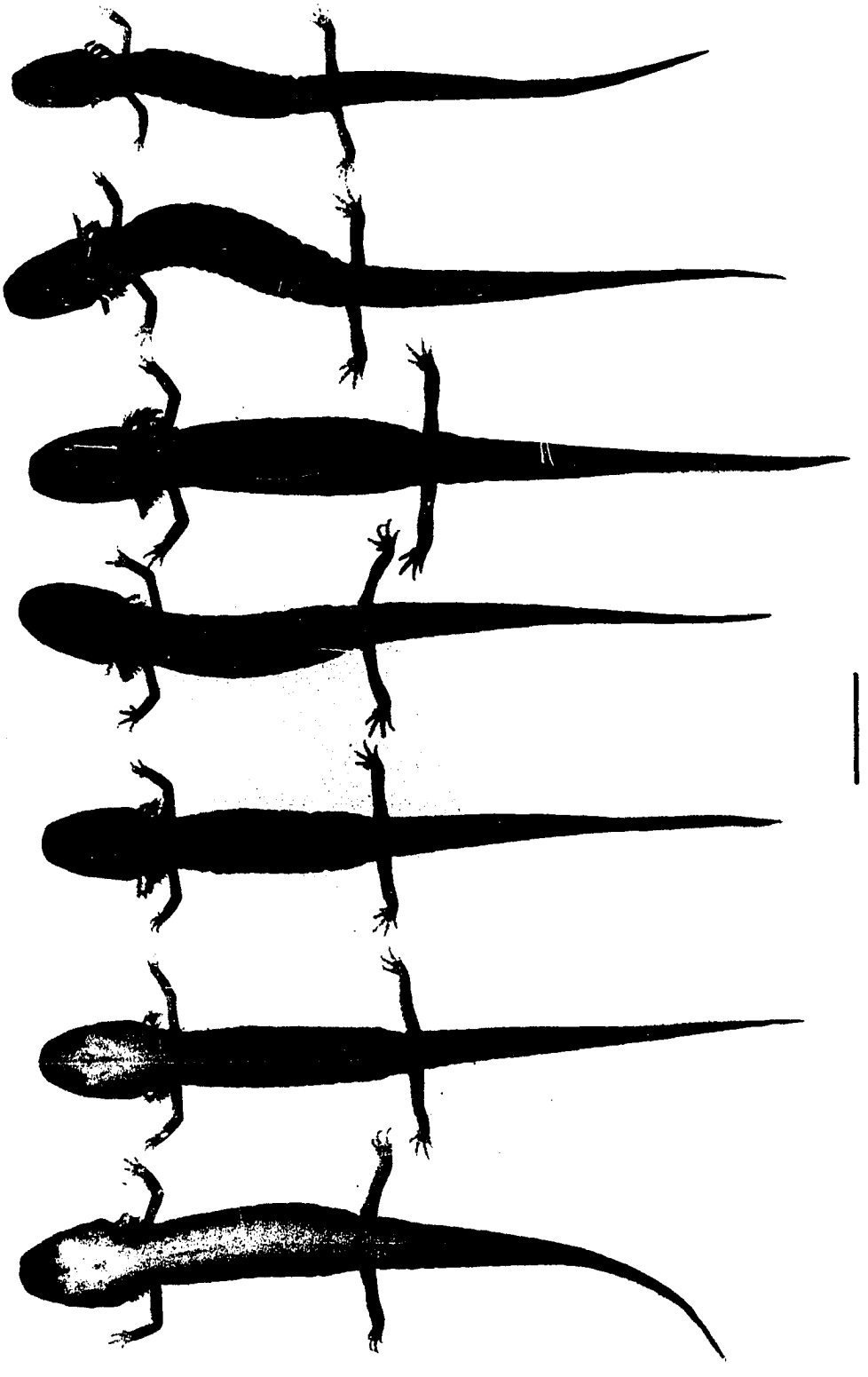

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Cascade Caverns and Cascade Sinkhole

Cascade Caverns and Cascade Sinkhole are closely associated components of a regional subterranean drainage system beneath the floodplain of Cibolo Creek in southern Kendall and Comal Counties. This drainage is developed on at least two levels in the lower Glen Rose limestone; the lower levels are usually flooded and are unexplored, but presumably they link the very numerous sinkholes on this plain into one or more major channels. This is usual in mature karstic regions (Howard, 1963; Smith, 1971). These channels convey groundwater towards the Balcones Fault Zone to the south and east, discharging at major springs. The upper levels of many of the caves of the Cibolo sinkhole plain contain small streams and pools resulting from local drainage and backflooding of the cave system during periods of heavy recharge. Salamanders occur in varying densities on these upper levels and are presumably derived in part from permanent populations below. Most of the known populations of E. tridentifera also occupy the Cibolo sinkhole plain to the east of Cascade Caverns; the nearest localities for E. tridentifera (Badweather Pit and Grossers Sinkhole) are only 5.6-6.0 km to the east in a seemingly homogeneous subterranean drainage network.

Eurycea latitans was described from a series of 21 specimens only two of which are now available from Cascade Caverns (Smith and Potter, 1946). Eleven additional specimens collected prior to 1950 are available, but several are in a poorly preserved state. Eight individuals collected in Cas-

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cade Sinkhole since 1965 are also at hand; several of these differ from earlier specimens and appear to represent a less advanced level of troglobitic specialization. As Figure 26 shows, these specimens are slender, with larger eyes and more pigmentation than the two early specimens illustrated. These recent individuals closely resemble specimens from several caves along the Guadalupe River to the north (see Fig. 32) which I refer to E. neotenes (Chapter IV).

Morphological Correlates of Secondary Contact

Individual Variability

Most of the characters showing directional change in the series of surface to advanced cave populations are cumbersome as indices of the degree of troglobitic specialization: they are either difficult to quantify (coloration, eye structure) or exhibit moderate ontogenetic allometry (proportions and tooth counts). The number of trunk vertebrae varies directionally through the adaptive trend of the Texas Eurycea and may serve as an index of specialization as well as being a simple indicator of unusual levels of individual variability. Advanced troglobitic Eurycea are short-bodied, all known populations of E. tridentifera being strongly modal at 14 trunk vertebrae (Sweet, 1977b). Nearly all surface-dwelling populations of E. neotenes have strong modes at 17 trunk vertebrae, as do all troglobitic populations currently referred to this species. No population modal at 15 trunk vertebrae is known; modes of 16 characterize the sam-

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Figure 26. Five specimens of Eurycea latitans from the Cascade Caverns system, Kendall County, Texas, illustrating apparent proportional differences between specimens from early (left pair) and recent collections. The coloration is lost in the early specimens as a result of poor preservation, which may also influence their apparent robustness. The scale bar = 10 mm.

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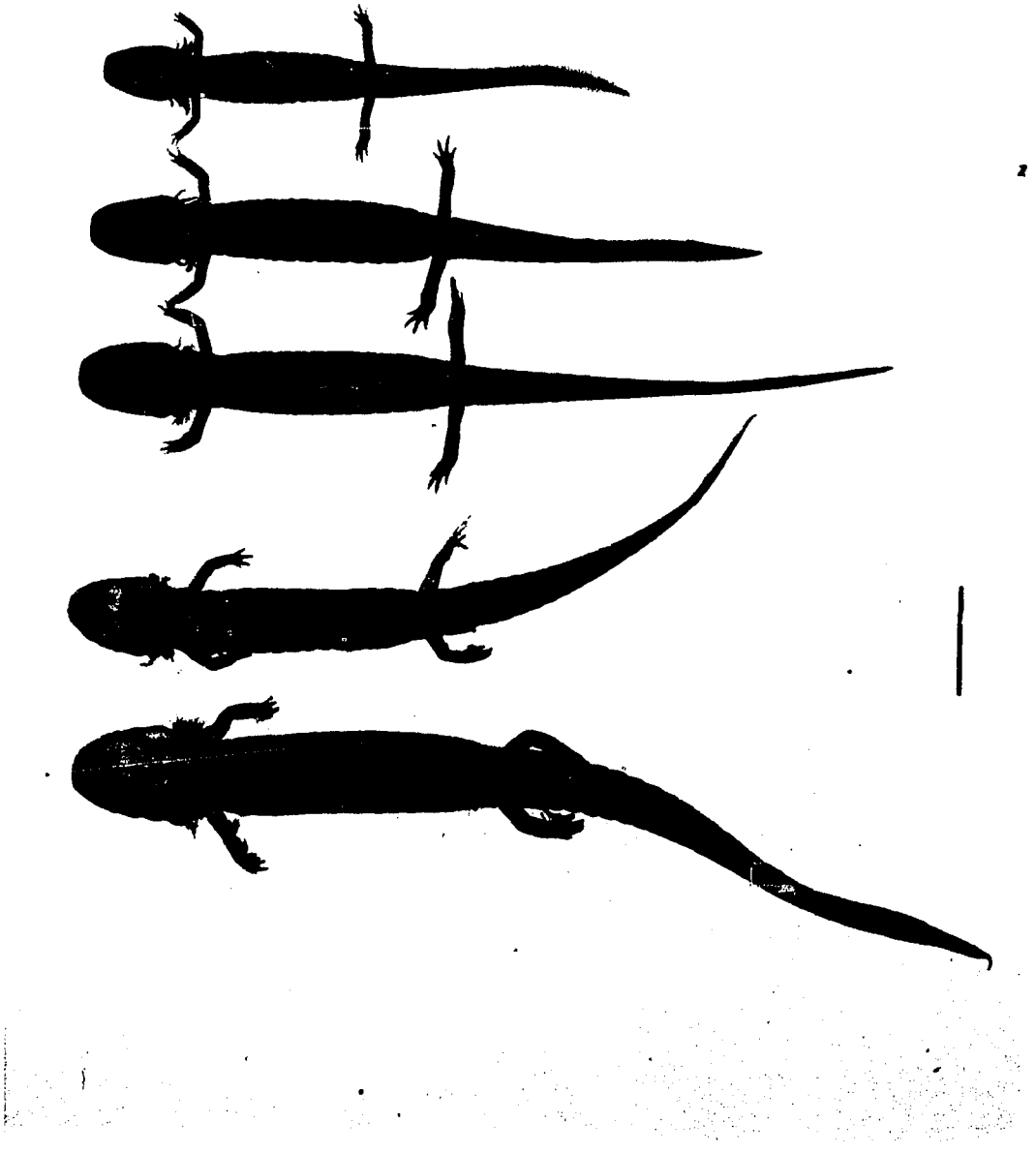

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ple of structurally intermediate specimens from Honey Creek Cave and three other troglobitic populations. One, E. sp., has a strong mode of 16; E. troglodytes, E. latitans and the Honey Creek Cave intermediates show considerable variability (Table 13). The variation in vertebral number seen in these samples is exceptional among 135 populations of surface and cave Eurycea surveyed in the course of a broader study of the group; data from several such populations are included in Table 13. The observed range in vertebral number in each of the three unusual populations overlaps both E. neotenes and E. tridentifera, and is consistent with an hypothesis of hybrid origin for these samples. The standard deviations of vertebral numbers are comparable among populations assigned to E. neotenes, E. sp., and E. tridentifera, but are substantially larger in the Honey Creek Cave hybrid sample, and in E. troglodytes and E. latitans. The clear distinction between epigean and troglobitic populations present at Honey Creek Cave permits the prior subdivision of this sample into three units; if not so divided the distribution of vertebral numbers would be: 13, 9; 14, 48; 15, 4; 16, 2; 17, 7, with a standard deviation of 1.05.

The degree of individual variation and character discordance in body proportions and numbers of teeth is reflected in the correlation coefficients of pairs of variables such as those listed in Table 14. The observed pattern is not the result of inequalities in sample size. While the degree of correlation in body proportions is generally high in the pop-

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Table 13. Distributions and standard deviations of number of trunk vertebrae in 18 samples of Texas *Eurycea*. Populations of *E. neotenes* are arranged in east to west sequence.

Species	Population	Number of Trunk Vertebrae 13	14	15	16	17	18	S.D.
E. neotenes								
	Krienke Spring				9	32	1	0.455
	Puter Creek				7	89	9	0.378
	Honey Creek Cave					6		0.000
	Cibolo Creek					96	13	0.336
	Fall Creek				5	206	12	0.188
	Seco Creek				4	42	7	0.456
	Mill Creek				9	163	2	0.247
	Ash Hollow				10	216	15	0.329
	Dutch Creek				5	120	4	0.265
E. neotenes X *tridentifera*								
	Honey Creek Cave			1	2	1		0.816
E. latitans								
	Cascade Caverns			5	8	6	1	0.847
E. troglodytes								
	Valdina Farms Sinkhole		1	4	20	14	1	0.808

E. sp.						
Travis County			2	35	3	0.357
E. tridentifera						
Honey Creek Cave	9	48	3			0.273
Badweather Pit	3	43	1			0.292
Grosser's Sinkhole	2	14	5			0.301
Kappelman Salamander Cave		5				0.000
Elm Springs Cave	1	7				0.354

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Table 14. Correlation coefficients of body proportions and numbers of teeth in 19 samples of Texas *Eurycea*. Average correlation coefficients were calculated through transformation to Z. Values marked with an asterisk are *not* significant at the 0.05 level.

Species	Population	N	HW/SL	HLL/SL	ED/HW	PM/HW	VO/HW	DT/HW	r
E. neotenes									
	Honey Creek Cave	6	0.90	0.94	0.76	0.78	0.58*	0.78	0.83
	Cibolo Creek	50	0.98	0.98	0.93	0.87	0.85	0.93	0.94
	Seco Creek	31	0.96	0.96	0.89	0.53	0.60	0.56	0.84
	Salamander Cave	8	0.90	0.63	0.82	0.40*	0.62	0.62	0.70
	Bender's Cave	38	0.96	0.96	0.75	0.77	0.76	0.75	0.87
	Deadman's Cave	15	0.99	0.98	0.95	0.91	0.95	0.92	0.96
	Alzafar Water Cave	14	0.99	0.91	0.85	0.86	0.86	0.85	0.91
	Tucker Hollow Cave	9	0.99	0.98	0.98	0.95	0.83	0.84	0.97
	Carson Cave	15	0.98	0.97	0.81	0.88	0.83	0.88	0.92
	Fourmile Cave	8	0.97	0.94	0.82	0.66	0.27*	0.59*	0.81
E. neotenes X *tridentifera*									
	Honey Creek Cave	4	0.88*	0.39*	0.51*	0.68*	0.91	0.85*	0.76*
E. latitans									
	Cascade Caverns	17	0.96	0.95	0.80	0.61	0.60	0.84	0.85
E. troglodytes									
	Valdina Farms Sinkhole	38	0.85	0.72	0.42	0.20*	0.24*	0.28*	0.51

E. sp.								
Travis County	34	0.93	0.91	0.68	0.61	0.73	0.56	0.78
E. tridentifera								
Honey Creek Cave	38	0.91	0.85	0.31	0.45	0.52	0.51	0.66
Badweather Pit	37	0.95	0.91	0.02*	0.75	0.61	0.60	0.74
Grosser's Sinkhole	17	0.86	0.86	0.10*	0.14*	0.36*	0.83	0.63
Kappelman Salamander Cave	4	0.98	0.90	0.84*	0.56*	0.76*	0.51*	0.84
Elm Springs Cave	8	0188	0.86	0.01*	0.49*	0.92	0.89	0.78

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ulations examined, the more specialized troglobites show reduced correlations of eye size and numbers of teeth with body size. This decrease is primarily related to a twofold increase in numbers of teeth within the adaptive trend, though the variance also increases in advanced troglobites. The eyes of E. tridentifera essentially cease growth at an early stage, and their size is not significantly correlated with body size. Intermediate troglobitic populations display lower correlation coefficients than do epigean populations, but retain significant positive allometry of eye size. In sum, fewer than 10% of the correlations lack statistical significance ($p < 0.05$) in the series of populations referred to E. neotenes, and in E. latitans and E. sp., whereas a third of the values in the E. tridentifera samples are not significant. This proportion increases to half of the values for E. troglodytes and two thirds of the values for the Honey Creek Cave intermediates, though the latter sample is too small for meaningful evaluation. At the least, the hypothesis of hybrid origin receives support to the extent that these two samples show less correlation among characters than is noted in more highly derived troglobites.

Discriminant Analysis

Discriminant analysis seeks to maximize the differences present in a character matrix representing two or more specified groups, producing character weightings which define the location of individuals in discriminant space through one or more linear functions. The discriminating power of the tech-

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nique can easily exceed the validity of its interpretation; discrimination of samples *per se* must be interpreted with special caution. The approach here is to use the results in a relative, comparative fashion in an effort to discern both unusual levels of within-group variation and instances of failure in the classification of specimens to their pre-assigned groups. The relative positions of specified groups in discriminant space are also of interest in analyses which encompass the range of an adaptive trend such as the series of troglobitic populations considered here.

Discriminant anaylses were performed with trios of population samples consisting of a morphologically intermediate sample and two geographically adjacent reference groups of *E. neotenes* and *E. tridentifera*. These taxa are the probable parents if hybridizing situations exist. Prior probabilities were considered equal, and all variables were entered concurrently. The following characters were employed: SL, HW, ED, HLL, TV, PM, VO and DT.

The presumed hybrid samples occupy intermediate positions on the first discriminant axis with respect to known or presumed parental reference groups (Figs. 27-29). Heavy loadings (Table 15) for number of trunk vertebrae, standard length, and hind limb length (in order of decreasing importance) characterize this axis, which is completely effective in separating the reference samples. Character loading coefficients are presented in Table 15. The first function explains 94%, 77% and 98% of the total variance in the Honey

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Table 15. Standardized character coefficients for 3 group discriminant analyses of 4 structurally intermediate samples of troglobitic *Eurycea*, and their *E. neotenes* and *E. tridentifera* reference groups.

Character	Honey Creek Cave		*E. troglodytes*		*E. latitans*		*E.* sp.	
	Fn 1	Fn 2	Fn 1	Fn 2	Fn 1	Fn 2	Fn 1	Fn 2
SL	0.249	1.446	1.609	1.543	1.992	2.775	1.692	-1.719
HW	0.453	-1.178	-1.835	-0.143	-0.602	-1.872	-1.304	3.505
ED	-1.673	-0.605	0.255	-0.473	1.114	-0.930	0.833	1.117
HLL	0.194	0.772	-0.841	-1.911	-2.416	0.365	-1.522	0.073
TV	-2.014	0.386	1.432	-1.200	2.098	-0.621	2.252	0.493
PM	0.259	-0.475	0.362	-0.807	0.173	-1.825	0.450	-0.466
VO	-0.240	-0.180	0.001	0.297	0.147	0.240	-0.012	-1.248
DT	-0.422	0.280	-0.720	-0.596	-1.038	0.090	-1.080	0.841

Creek Cave, Valdina Farms Sinkhole, and Cascade Caverns populations and their reference groups. A second discriminant function explains all of the remaining variance in each data set, with loadings distributed throughout the suite of characters in no apparent pattern. Scatter plots of individual scores on the two discriminant axes are presented in Figures 27-29, displaying the relative positions and degree of dispersion of the three intermediate samples and their reference groups. A fourth plot of the values of the adaptively intermediate yet structurally homogeneous E. sp. is also shown (Fig. 30). The samples of E. tridentifera, E. neotenes and E. sp. are more homogeneous than the samples of E. troglodytes, E. latitans and the Honey Creek Cave intermediates.

When each of the three samples (references and intermediate) is specified, the posterior probabilities of membership in the assigned groups can be evaluated for each individual. All specimens in the reference groups are properly allocated in these a posteriori tests, but eight individuals of the four intermediate samples are found to have higher probabilities of association with a reference group than with their assigned group. One of four intermediates is misclassified with E. tridentifera in the Honey Creek Cave analysis, and four of 38 E. troglodytes are misclassified, three with E. tridentifera and one with E. neotenes. Two specimens of E. latitans and one specimen of the undescribed species are misclassified with E. neotenes. A reexamination of the misclassified specimens assigned to E. tridentifera

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Figure 27. Scatter plot of individual scores on two discriminant axes for specimens of *Eurycea* from Honey Creek Cave. Crosses represent *E. neotenes* and squares denote *E. tridentifera*; the structurally intermediate individuals presumed to be hybrids are indicated by diamonds. Asterisks indicate group centroids.

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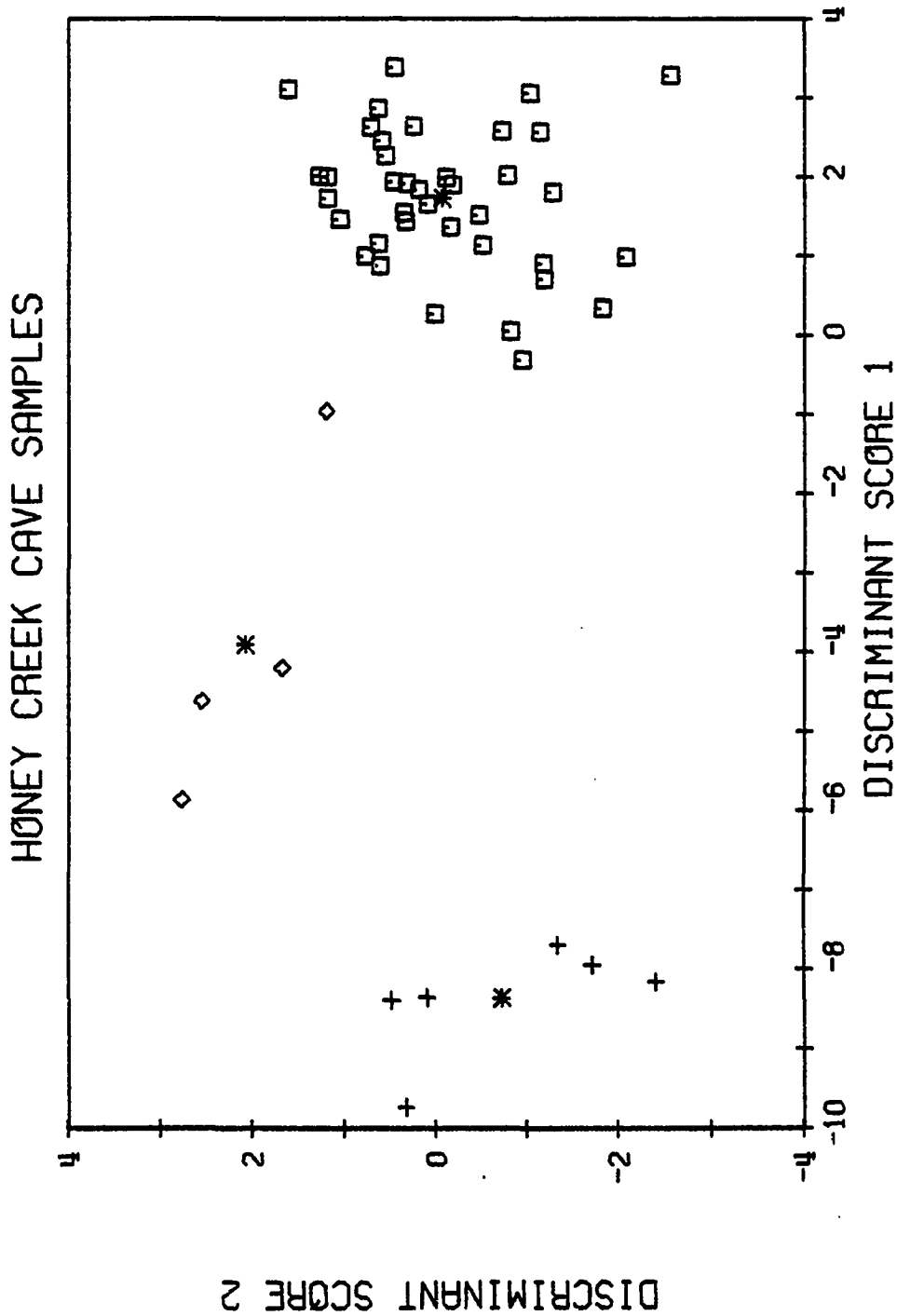

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Figure 28. Scatter plot of discriminant scores for specimens of *Eurycea troglodytes* (diamonds), Seco Creek *E. neotenes* (crosses), and Badweather Pit *E. tridentifera* (squares). Filled diamonds denote *E. troglodytes* collected in 1972, 1973, and 1974. Asterisks indicate group centroids.

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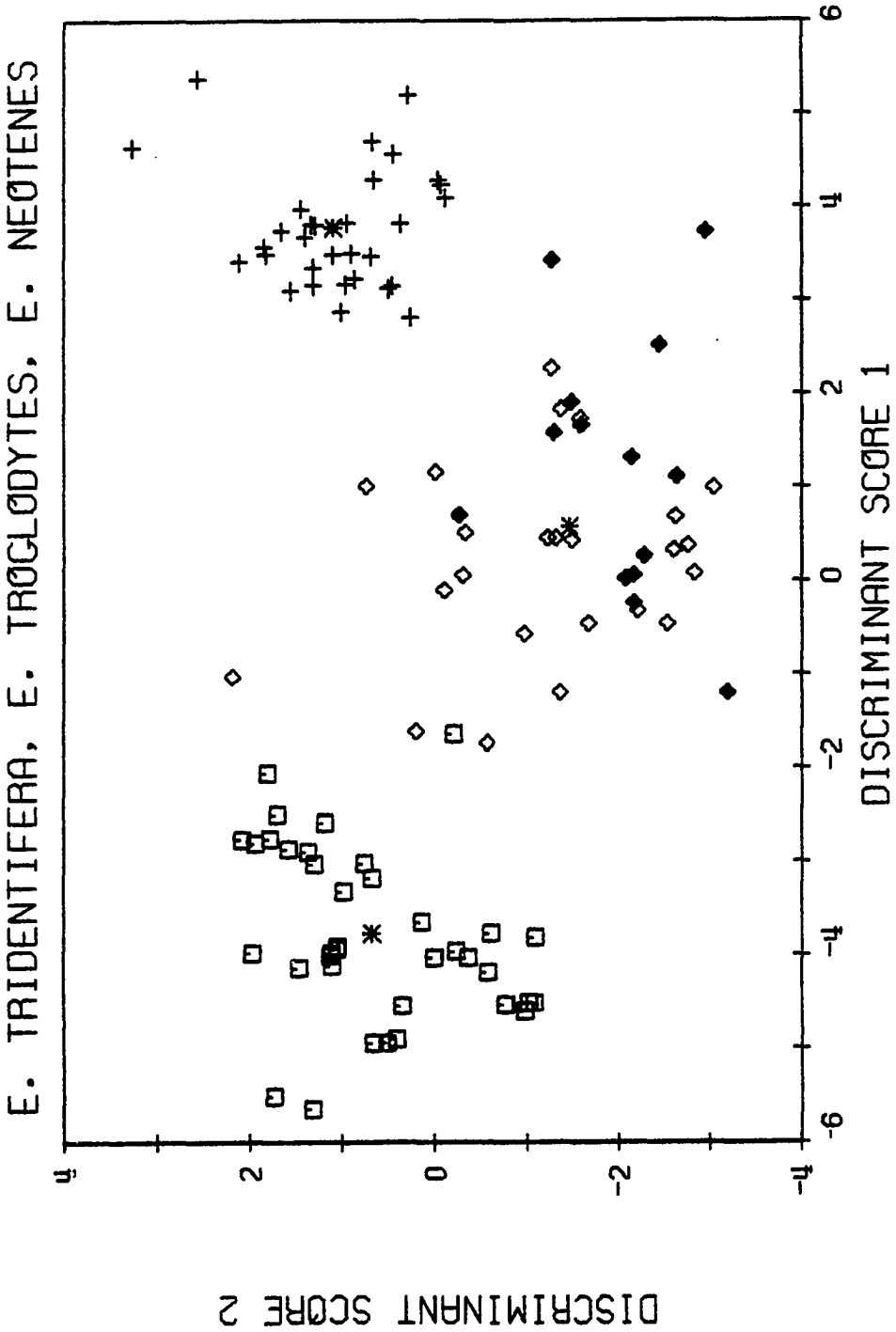

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Figure 29. Scatter plot of discriminant scores for specimens of *Eurycea latitans* (diamonds), Cibolo Creek *E. neotenes* (crosses), and Badweather Pit *E. tridentifera* (squares). Filled diamonds indicate *E. latitans* collected since 1965. Asterisks denote group centroids.

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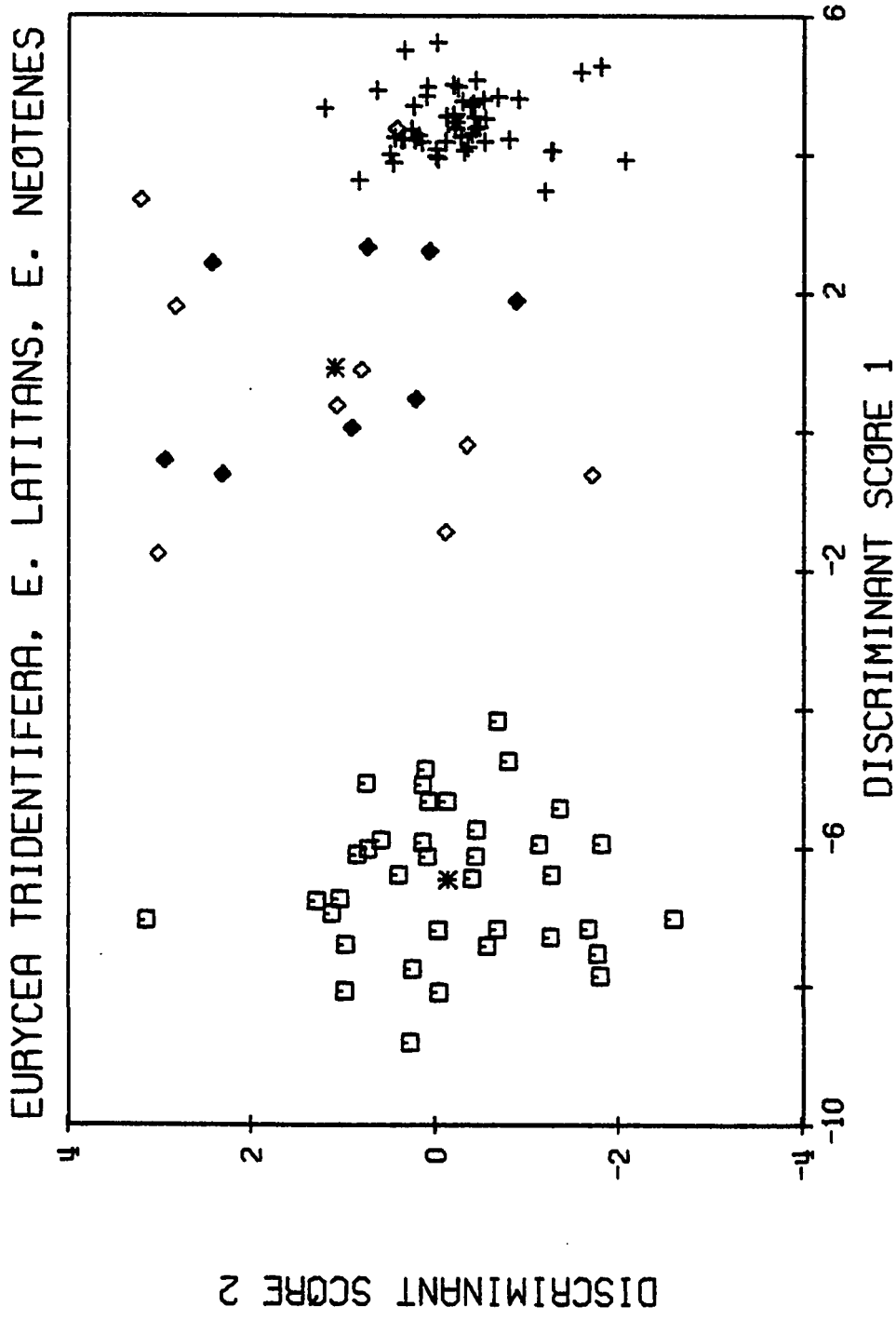

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Figure 30. Scatter plot of discriminant scores for specimens of *Eurycea* sp. (diamonds), a troglobitic population comparable to *E. troglodytes* and *E. latitans* in degree of specialization. Reference groups are Seco Creek *E. neotenes* (crosses) and Badweather Pit *E. tridentifera* (squares). Asterisks indicate group centroids.

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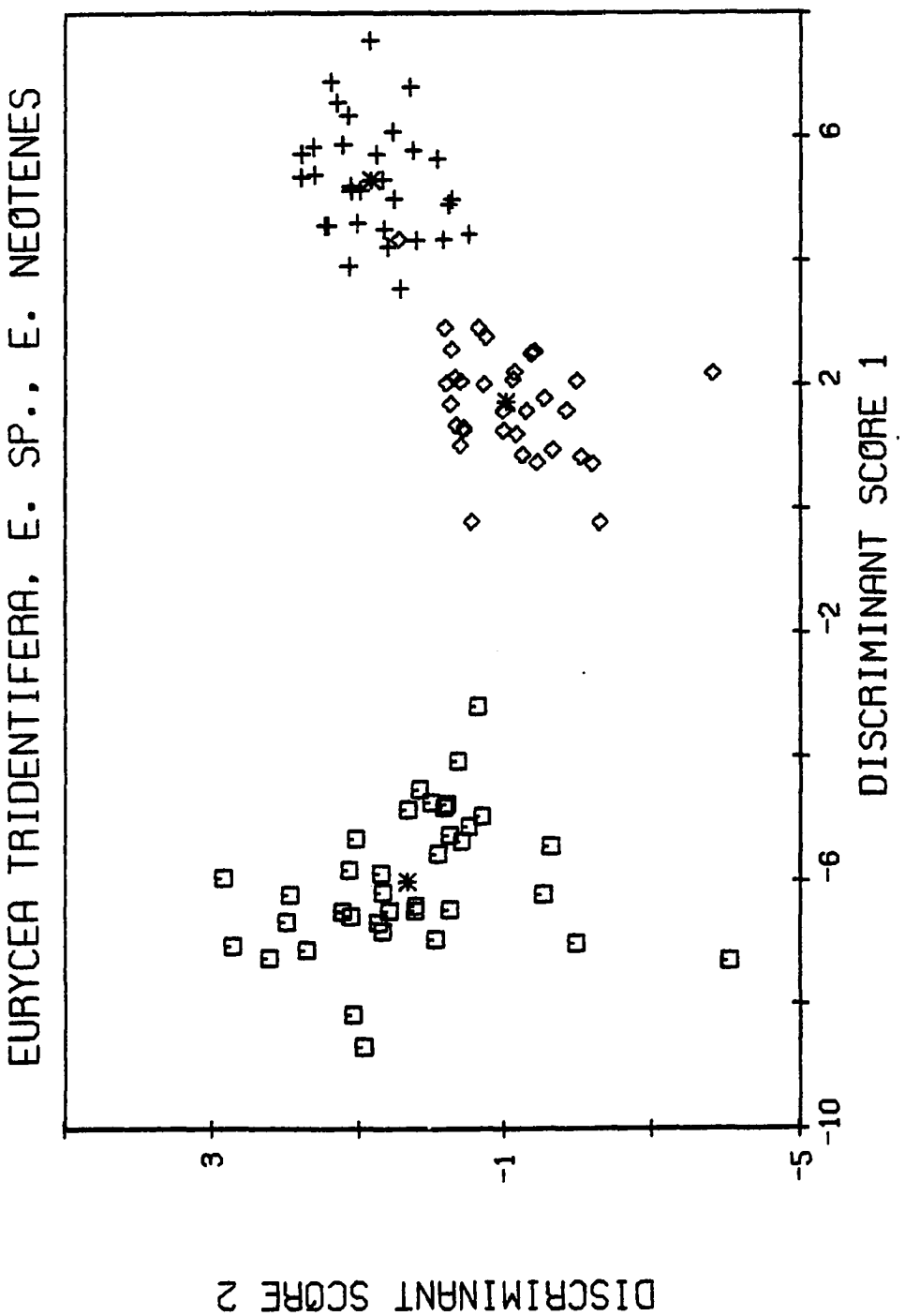

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does not support the possibility that they were initially misclassified (misidentified); considerable differences in coloration and skull proportions exist between E. tridentifera and the misclassified individuals. The individuals of E. troglodytes and E. latitans misclassified as E. neotenes are not easily distinguished from that form, and may represent immigrant individuals of this surface-dwelling species.

By the specification of the reference groups alone, the individuals constituting the intermediate samples can be forced to assort on the basis of the simple majority of their affinity. In this analysis three intermediates from Honey Creek Cave sort with E. neotenes and one with E. tridentifera. This majority is also reflected in the forced assortment of the E. troglodytes sample: 27 specimens are aligned with E. neotenes, and 11 with E. tridentifera. All but two of the 17 E. latitans sort with E. neotenes. As a further step, the samples of E. troglodytes and E. latitans can be divided into three and two groups, respectively, on the basis of collection date to evaluate the possibility that these populations have changed in composition during the past few decades. When this is done with the E. troglodytes sample, a clear trend towards the influence of E. neotenes emerges in the ratio of forced assortment of E. tridentifera:E. neotenes as follows: 1957, 7:8; 1967, 2:4; 1972-1974, 1:13. Three specimens of unknown collection date are omitted. Using the results of the three-group discrimination, the distributions of each of these subgroups in discriminant space can be com-

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pared by multivariate analysis of variance. These tests show that the shift seen in the 1972-1974 subgroup represents a significant departure ($p < 0.01$) from the distributions of the two earlier subgroups. The 1957 and 1967 subsamples do not differ from one another significantly. The four E. troglodytes misclassified in the three-group analysis consist of two from the 1957 subgroup and one from the 1967 subgroup having higher posterior probabilities of assortment with E. tridentifera than with E. troglodytes, and one specimen from the 1972-1974 subgroup which is aligned with E. neotenes.

The situation is less clear in the E. latitans sample, which can be divided into subgroups of nine specimens collected between 1933 and 1959, and eight taken since 1965. The two specimens which assort with E. tridentifera in the two-group analysis are from the earlier subgroup; one specimen from each subgroup is misclassified with E. neotenes in the three-group discrimination. The distributions of individual scores by subgroup are not significantly different in this case, suggesting that the composition of this population has been more stable than has that of E. troglodytes.

The general outcome of these tests is that the three suspected hybrid samples presently share greater affinity with E. neotenes than with E. tridentifera. In both cases where temporal subdivision of the samples is possible, individuals aligned with E. tridentifera strongly predominate in the early collections, amounting to 9 of the 12 so assorted

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in the two-group tests, and four of the five misclassified in the three-group analyses. Because early samples comprise about half of the available material in each case, the observed trend is probably not an effect of disparate sample sizes.

Character Discordance

The requisite evidence of phenotypic intermediacy and increased individual variability in hybrid situations is usually to be had through correlation and discriminant analyses, construction of hybrid indices, and the like. In the present case this evidence is suggestive but not sufficient, except perhaps where parental populations are sympatric as at Honey Creek Cave, because nothing precludes the existence of structurally intermediate populations of nonhybrid origin. In fact, at least one is known (E. sp.). Further, only arguments by analogy can be advanced to counter the suggestion that increased levels of variability may validly characterize adaptively intermediate populations. A third type of phenotypic evidence for hybridization is not directly derivable from the standard techniques and is seldom distinguished from individual variability (see, for example, Jackson [1973] and the recent review of such evidence by Schueler and Rising [1976]). This evidence consists of documentation of the discordant recombination of parental character states in hybrid individuals and is perhaps the only unambiguous phenotypic evidence for hybrid origin of samples in which the presumed

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parental taxa are rare. Measurements of individual variability may reflect this discordance, but they generally fail to distinguish between heterogeneity among individuals comprising a sample and heterogeneity in the set of character states in individuals. This distinction is critical, as only the latter property is an accurate index of character discordance.

When certain assumptions discussed below are satisfied, the degree of agreement among character states in individuals can be evaluated by Kendall's coefficient of concordance (Siegel, 1956). This nonparametric function determines the association among several rankings of a series of objects, with values ranging from 0 (no association) to 1. The concordance value is the ratio of the sum of squared deviations of specimen rank sums to the maximum possible sum of squared deviations.

Two general limitations of the technique apply to morphological data: the independent variable should be the same for all characters employed, and the distribution of cases should be ordinal or otherwise uniform in nature. Size is the obvious independent variable in most applications at the population level, although the suite of characters comprising an adaptive trend could be employed in a comparison among taxa. In the present application each specimen in a sample is assigned a rank for each of the seven size-dependent characters previously used; trunk vertebral number is not correlated with ontogenetic size change and has been

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omitted. In a perfectly concordant sample each specimen would have a consistent, uniform rank across the set of characters. As the degree of size dependence of character states diminishes, heterogeneity will appear in the individual rank scores, reducing the concordance value of the sample. Used in this way, the concordance value is essentially a measure of the degree of homogeneity among the allometric relationships of the variables within a sample of specimens. Populations having a uniform set of allometric relationships will be more nearly concordant than will those in which sets from different parental taxa are variously recombined.

Uniformity in size distribution within samples is an important consideration when using allometric variables. Discordance will not be detected in a rank-ordering of cases in which the size increment between specimens exceeds the value at which the rank-order results of different allometric relationships are inseparable. For example, while the relative limb lengths of E. neotenes and E. tridentifera differ considerably, a composite sample containing both species might still be estimated to be highly concordant if the size increment between individuals was 5 mm or more. Concordance will be overestimated in such cases. Concordance may be underestimated in cases of tightly-packed size distributions owing to the rank-order consequences of measurement error or individual variability in characters with moderate size-dependence.

The results of several analyses of concordance in popu-

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lations of the Texas Eurycea are presented in Table 16 . Average size increments between individuals can be estimated from the sample size and size range data included; in samples of more than 10 specimens this value ranges from 0.5 to 2.7 mm ($\bar{x}$, 1.18 mm), and is somewhat larger (1.6-3.8 mm; $\bar{x}$, 2.63 mm) in the remaining smaller samples. Concordance values and average size increments are not significantly correlated, whether in the sample as a whole ($r = 0.24$), in samples larger than 10 ($r = 0.46$) or less than 10 ($r = 0.52$), or in the set excluding the three suspected hybrid samples ($r = 0.37$). The number of individuals tied in sums of character ranks is indicated for each sample as a measure of the degree of clustering. The percent of tied scores and concordance value in the sample as a whole are not significantly correlated ($r = 0.23$). These indices demonstrate reasonable homogeneity among the larger samples and suggest that the results of the concordance tests are comparable. Seven samples of less than 10 specimens each are of interest to the questions examined and are included, despite the fact that two of them may approach the dispersion limitations previously discussed. Five of these samples have average size increments similar to those of the larger samples and lack tied scores; the concordance values for the Tucker Hollow Cave and Elm Springs Cave samples are probably inflated owing to relatively high average size increments (3.8 mm in each case). The significance of concordance values can be evaluated by transformation to chi-square (Siegel, 1956);

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Table 16. Values of Kendall's Coefficient of Concordance and related data for 19 samples of Texas *Eurycea*. Ties column refers to the number of individuals having tied scores in sums of character ranks. Size range is expressed in standard length. Asterisk marks one concordance value which is not significantly different from zero ($p>0.05$); the remaining values are highly significant ($p<0.01$).

Species	Population	N	Ties	Size Range	Coef. Conc.
E. neotenes					
	Honey Creek Cave	6	0	17.0-13.6	0.77
	Cibolo Creek	50	9	16.0-38.5	0.87
	Seco Creek	31	0	20.8-37.0	0.80
	Salamander Cave	8	0	26.0-43.7	0.69
	Bender's Cave	38	2	18.6-48.5	0.81
	Deadman's Cave	15	0	19.6-48.5	0.94
	Alzafar Water Cave	14	2	15.0-53.0	0.84
	Tucker Hollow Cave	9	0	15.0-45.4	0.86
	Carson Cave	15	2	17.4-41.6	0.88
	Fourmile Cave	8	0	29.8-42.2	0.65
E. neotenes X *tridentifera*					
	Honey Creek Cave	4	0	29.0-37.8	0.12*
E. latitans					
	Cascade Caverns	17	0	9.5-47.8	0.74

E. troglodytes				
Valdina Farms Sinkhole	38	4	22.5-43.6	0.37
E. sp				
Travis County	34	4	16.0-38.5	0.70
E. tridentifera				
Honey Creek Cave	38	4	18.8-37.2	0.48
Badweather Pit	37	8	19.7-46.0	0.54
Grosser's Sinkhole	17	2	25.3-39.1	0.42
Kappelman Salamander Cave	4	0	23.0-38.2	0.81
Elm Springs Cave	8	0	24.2-38.7	0.52

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all values save that of the Honey Creek Cave intermediate sample reflect highly significant association among the sets of rankings.

A comparison of Tables 14 and 16 shows that the same patterns are reflected by both parametric and nonparametric methods; the results of the two are significantly associated ($r_s = 0.93$, $t = 9.79$) in a Spearman rank correlation test. A relatively high order of concordance characterizes populations referred to E. neotenes, E. latitans, and E. sp. in comparison to E. tridentifera; again E. troglodytes and the Honey Creek Cave intermediates are seen to be the least homogeneous samples. There is no significant association among character states in the latter sample, a condition supporting the designation of these individuals as hybrids. The association is low (though significant) in E. troglodytes, and the same conclusion is supported, though the population value is not unlike the lower values noted among populations of E. tridentifera. This conclusion derives from the observation that character states are less concordant in this moderately specialized troglobite than in its highly specialized congener. Concordance values indicate that E. latitans is not differentiable from E. neotenes and E. sp. in the degree of association among character states.

As previously noted, body proportions other than eye size are strongly correlated in most populations; E. tridentifera differs from E. neotenes in the degree of size dependence in eye and tooth characters. Reduced size dependence

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or concordance values for these characters in the suspected hybrid samples thus provides somewhat equivocal evidence for the occurrence of hybridization. However, hybrids should show reduced correlation and concordance in body proportions as well as in eye and tooth characters in comparison to the presumed parental populations. Examination of Table 14 shows this to be the case for E. troglodytes and the Honey Creek Cave material; calculation of a reduced set of concordance values based only upon SL, HW, and HLL confirms this expectation in these samples. In the Honey Creek Cave samples reduced concordance values are as follows: E. neotenes, 0.90; E. tridentifera, 0.84, and presumed hybrids, 0.81 (the latter value is not significant at the 0.05 level). Eurycea troglodytes has a reduced concordance value of 0.76 in comparison to values of 0.95 and 0.92 for the Seco Creek E. neotenes and Badweather Pit E. tridentifera reference samples. The hypothesis is not confirmed in the case of E. latitans, which has a reduced concordance value of 0.97 in comparison to the Cibolo Creek E. neotenes (0.98) and Badweather Pit E. tridentifera reference samples. The reduced value for the undescribed form is 0.92.

Reproductive Condition

Gross examination of the gonads and of sex ratios in the individuals comprising the presumed hybrid samples gives no indication of reduced reproductive capability. As is the case in several other genera of plethodontid salamanders,

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males of the Texas Eurycea exhibit testis lobation; the number of lobes is correlated with body size (Bruce, 1976), consistent with the generality that the lobes represent successive annual reproductive cycles (Humphrey, 1922). Each of the three presumed hybrid samples contains males with at least three testis lobes of apparently normal structure. Brandon (1971) concluded that his small samples of E. troglodytes and E. latitans included sexually active males. Further, Bogart (1967) observed normal meiotic karyotypes representing metaphase II and anaphase II in testis preparations from E. troglodytes. This strongly indicates that male E. troglodytes undergo normal spermatogenesis though it provides no evidence concerning spermiogenesis. Females with normal complements of large (1.4-1.7 mm) yolked ova are represented in each of the three samples, as are specimens in earlier stages of oogenesis.

The sex ratio is equal in the Honey Creek Cave sample, but males predominate in both E. troglodytes (14:9) and E. latitans (14:6); neither distribution deviates significantly from equality by chi-square test. The predominance of males (17:3) reported in the type series of E. latitans (Smith and Potter, 1946) together with sexed specimens from later collections (total, 30:5) represents a significant deviation from a 1:1 ratio. The data from the type series are not entirely reliable,as Brandon (1971) has shown that the sex of the holotype was incorrectly determined. The six individuals from this series which have been sexed by internal examination

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are included in the first-mentioned sex ratio. Apart from this possible imbalance, E. troglodytes and E. latitans are apparently reproductively competent; together with the Honey Creek Cave intermediates, individuals of these populations reach large size and generally contain large fat bodies as well as gonads of normal morphology.

Discussion

Possible Competitive Exclusion at Honey Creek Cave

Eurycea neotenes may have been displaced or, as seems more likely, prevented from colonizing the subterranean portion of Honey Creek Cave by E. tridentifera. Competitive exclusion is difficult to document with the best of evidence, and that available here is far from complete, consisting of correlations and analogies based in distributional and morphological data. However to the extent that these classes of data may be causally interrelated an interpretation of competitive exclusion is an option. These data are presented below, following a brief background discussion of the geomorphology of the region involved.

As noted in Chapter II the entrenchment of the Guadalupe River in Kendall and western Comal counties has resulted in the development of numerous local subterranean drainages. The incised river bed now lies 50-110 m below the surface of its broad Pleistocene valley (George, 1952), which has an area of about 700 square kilometers (Fig.31). Surface drainages and springs are poorly developed on the valley floor and

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tend to be intermittent upstream from their short ravines bordering the river; consequently, epigean populations of Eurycea are infrequent on the valley floor (Chapter IV). The valley surface is developed on the hard and lithically uniform but soluble lower member of the Glen Rose Limestone, which is underlain by the clayey dolomites and sandstones of the Hensel Sand (Stricklin, Smith and Lozo, 1971). The Hensel is resistant to solutional erosion, and its upper surface forms a base level for the cave systems of the middle Guadalupe valley, which originate in sinkholes on the valley surface and drain towards the river canyon (Smith, 1971). These systems span a broad range in size and complexity, from linear passages $<$ 200 m in length with one to several local sinkholes (sites 2,3,8,9 and 12; Fig. 31), to large branching drainages $>$500 m in length, which receive surface runoff through a large number of sinkholes (sites 6,7,13 and 14). Most of these subterranean drainages open into the heads of tributary ravines, and all but one occur at the contact between the Hensel Sand and the overlying lower Glen Rose Limestone (Smith, 1971; Fig. 31); site 16 is a small cave developed in the Cow Creek limestone underlying the Hensel Sand. Water emerges from either the cave entrance or from adjacent rock rubble in sites 2-14 and 16; site 1 is a sinkhole tributary of a presently unlocated spring, and site 15 is a spring lacking an associated cave. Most of these outlets, as reported by local landowners, flow permanently (George, 1952; Reeves, 1967), and most of them appear to provide suitable

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Figure 31. Map of the middle section of the Guadalupe River showing localities discussed in the text. The approximate limits of the ancestral valley are indicated by the shaded line; the stippled region along the river represents the outcrop of the Hensel Sand and Cow Creek Limestone. Filled circles denote caves and associated springs inhabited by Eurycea; populations are not known from the sites indicated by open circles. The filled square locates the only strictly epigean population of E. neotenes in the Guadalupe canyon. This figure is an enlargement of the northeastern corner of Figure 23. Sites indicated on the figure are: 1, Behr's Cave; 2, Victor Phillip Water Cave; 3, Golden Fawn Cave; 4, Alzafar Water Cave; 5, Prassell Ranch Cave; 6, Deadman's Cave; 7, Spring Creek Cave; 8, Fourlevel Water Cave; 9, Little Water Cave; 10, Edge Falls Cave; 11, Honey Creek Cave; 12, Simmons Creek Cave; 13, Bender's Cave; 14, Plumly Ranch Cave; 15, Puter Creek Spring; 16, Rebecca Creek Spring.

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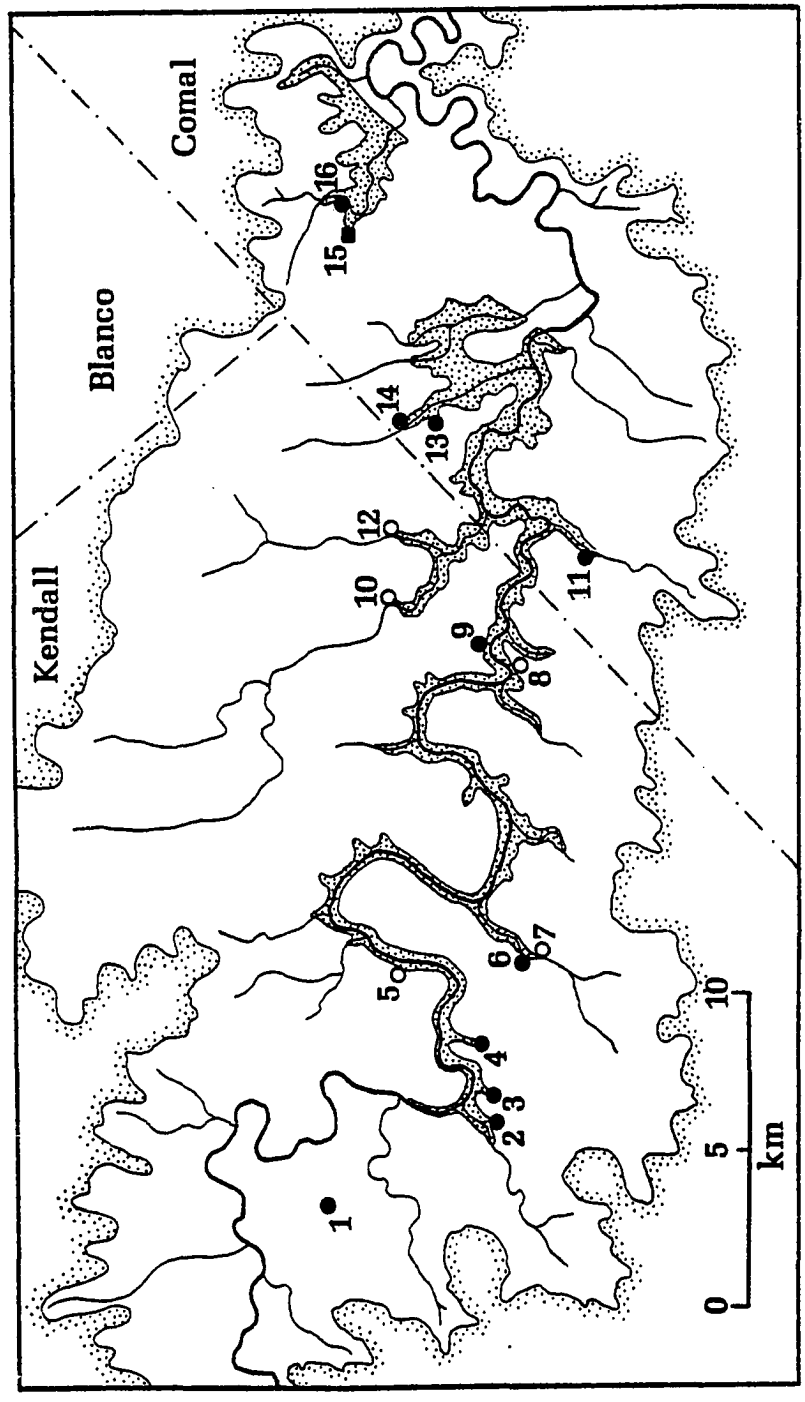

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habitat for E. neotenes on the basis of experience elsewhere on the Edwards Plateau.

Twenty springs in the Guadalupe canyon were examined in the course of this work: 15 are associated with caves, and 5 are not. Populations of E. neotenes were found in 3 of the cave outlets (sites 2, 11 and 16) and one spring (site 15). In each of the cave outlets one or more salamanders were collected or observed within the cave as well.

All of the cave localities reported here have been visited by members of the Texas Speleological Survey, Austin (Reddell, 1964; T.S.S. files), and by me. Records of Eurycea from these caves are given by Baker (1961), Mitchell and Reddell (1965) and Reddell (1965); site 1 (Behr's Cave) has not been previously reported to contain Eurycea. Eleven populations of Eurycea are known from the 15 caves (sites 1-4, 6, 9, 11, 13, 14 and 16); eight of these populations are exclusively troglobitic. A disjunct population of E. tridentifera occurs in Honey Creek Cave (site 11); I refer the remaining populations to E. neotenes (but see Reddell, 1967, and Mitchell and Smith, 1972, who feel that other species may be involved). Sites 5 (Prassell Ranch Cave) and 7 (Spring Creek Cave) contain numbers of predatory fishes (Jones and Hettler, 1959; T.S.S. files) and probably lack populations of Eurycea. Sites 8, 10 and 12 were each examined once, and may prove to be inhabited by Eurycea when more thoroughly surveyed.

Eurycea neotenes tends to inhabit caves rather than

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springs in the Guadalupe canyon, with populations known from 20% of the surveyed springs versus 77% of the suitable caves (excluding sites 5 and 7); further, every spring-dwelling population with access to a cave also occurs within the cave. The occurrence of a predominantly surface dwelling population of E. neotenes at Honey Creek Cave is thus unusual, but not unique within the region. These distributional data are consistent with an hypothesis of competitive exclusion between E. neotenes and E. tridentifera at this site, but cannot be considered to be strong supporting evidence without a demonstration that this population of E. neotenes is less adapted to subterranean life than other surface dwelling populations.

Troglobitic populations of E. neotenes in the Guadalupe region appear to differ in several respects from epigean populations of this area and elsewhere. Particularly noticeable is a tendency for reduction in the dark dorsal mottling characteristic of epigean E. neotenes (Brown, 1967; Barrett and Benjamin, 1977), together with a darkening of the dorsal ground color from tan to light brown. Specimens from these troglobitic populations reach a larger size (to about 55 mm SL) than is known for epigean specimens (maximum about 40 mm SL); the eyes are reduced in size, the limbs are relatively long, and the head is relatively large and depressed. Ninety percent of the 252 specimens of E. neotenes available from sites 1-16 have 17 trunk vertebrae. Representatives of the 10 populations discussed here are illustrated in Figure

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32.

The apparent proportional differences among populations of E. neotenes were examined by discriminant analysis of 12 characters (SL, HLA, HLB, HLC, HW, ED, IOD, HLL, AG, PM, VO and PAL). Complete data sets were available for 151 specimens from 9 populations, as noted previously. No specimens are available from Little Water Cave (site 9), or Plumly Ranch Cave (site 14). With each of the 9 specified populations, the first 3 discriminant functions explain 93% of the total sample variance (64%, 21%, 8%); the remaining functions do not contribute significantly to the solution. The chief discriminating variables (Table 17) are head shape, eye size and hind limb length. The distribution of these populations on the first two discriminant functions is shown in Figure 33. These functions result in the correct classification of 71% of the specimens to population; the pattern of misclassification is informative. None of the E. neotenes from Honey Creek Cave (site 11) is misclassified, and none of the 24 misclassified specimens from the three other spring localities (sites 2, 15 and 16) is assigned to a troglobitic population. Twenty of 72 specimens from the 5 troglobitic populations (sites 1,3,4,6 and 13) are misclassified: 17 are assigned to other troglobitic populations, and 3 are assigned to epigean populations. This pattern suggests that the troglobitic and epigean populations form differentiable groups; a second discriminant analysis on this basis allocates 99% of the specimens to the correct habitat category. Again, no

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Figure 32. Photograph of representative specimens of *Eurycea* from 9 localities in the Guadalupe canyon, showing the pattern and proportional differences between troglobitic (specimens *a* to *e*) and epigean (*f* to *i*) populations discussed in the text. Specimens *a* to *i* are *E. neotenes*; specimen *j* is *E. tridentifera*. The largest available specimen from each locality is represented; scale bar equals 10 mm. The sequence of specimens in the figure corresponds to the positions of group centroids in Figure 33, as follows: *a*, Bender's Cave (site 13, MVZ 120501); *b*, Deadman's Cave (site 6, MVZ 121382); *c*, Alzafar Water Cave (site 4, MVZ 121369); *d*, Behr's Cave (site 1, MVZ 121392); *e*, Golden Fawn Cave (site 3, MVZ 121376); *f*, Victor Phillip Water Cave (site 2, MVZ 121206); *g*, Rebecca Creek Spring (site 16, MVZ 120274); *h*, Puter Creek Spring (site 15, MVZ 120278); *i* and *j*, Honey Creek Cave (site 11, MVZ 120383 and 120544). The sequence *a* - *j* reads from upper left to lower right.

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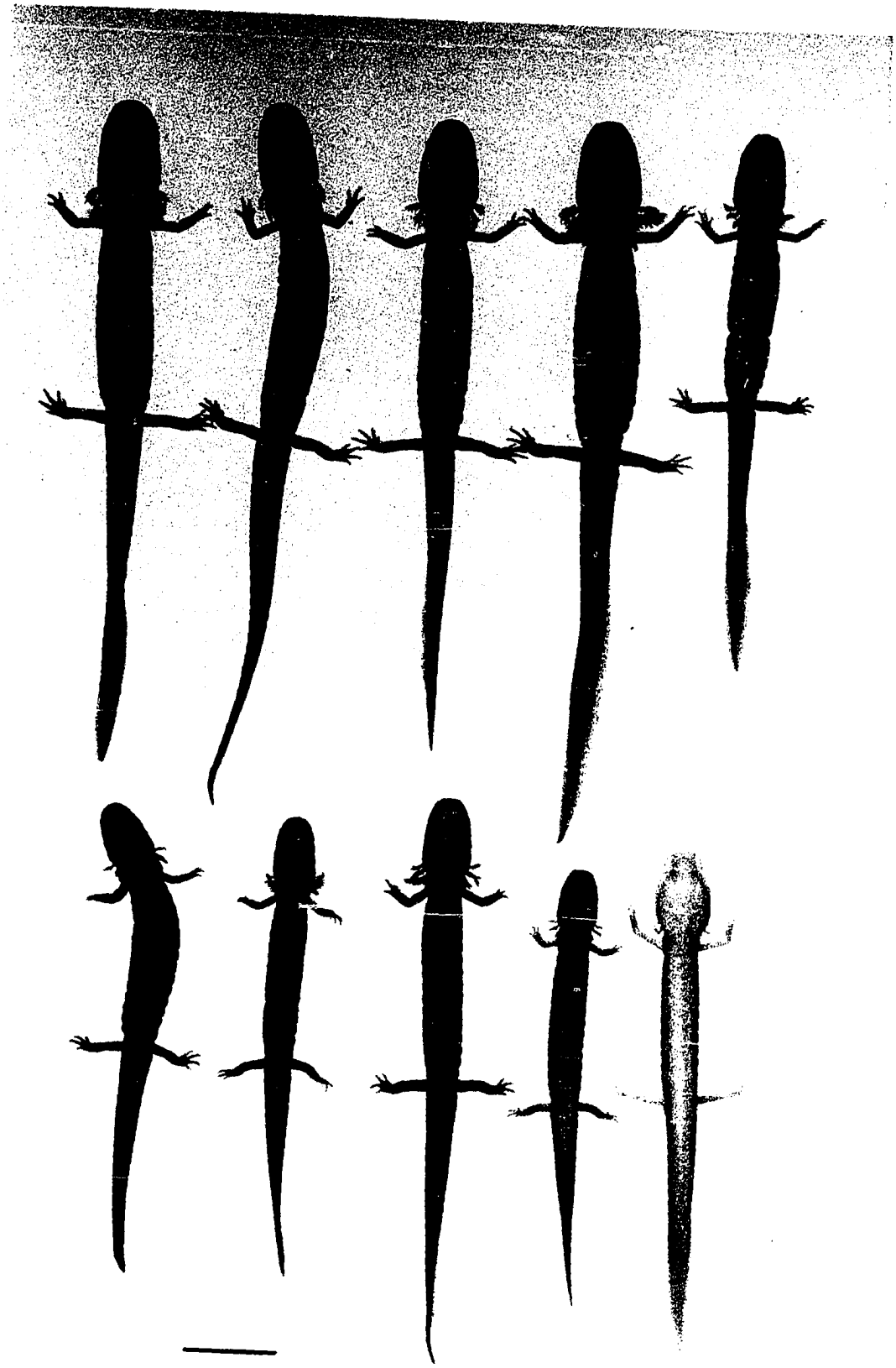

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Table 17. Standardized character coefficients for 9 and 2 group discriminant analyses of *Eurycea neotenes* from the Guadalupe River canyon, Comal and Kendall Counties, Texas.

Character	9 Groups Function 1	9 Groups Function 2	9 Groups Function 3	2 Groups Function 1
SL	-0.606	-6.276	0.978	-0.994
HLA	0.128	-1.432	-0.751	0.287
HLB	-1.632	3.353	1.669	-2.619
HLC	-1.211	2.816	-4.903	0.344
HW	-1.124	-0.922	2.881	-1.609
ED	1.686	1.893	0.241	1.389
IOD	2.208	0.471	-0.023	2.186
HLL	-1.345	-0.405	2.015	-1.532
AG	1.945	0.877	-2.362	2.484
PM	-0.054	-0.126	-0.475	0.359
VO	-0.661	-0.710	1.524	-0.925
PAL	-0.103	0.418	-0.620	0.148

Figure 33. Comparison of 9 population samples of *Eurycea neotenes* from the Guadalupe canyon by discriminant functions. Minimum convex polygons enclose the distribution of specimens from each population, numbered as in Figure 31; asterisks indicate group centroids, and the two habitat subgroups discussed in the text are demarcated by heavy lines.

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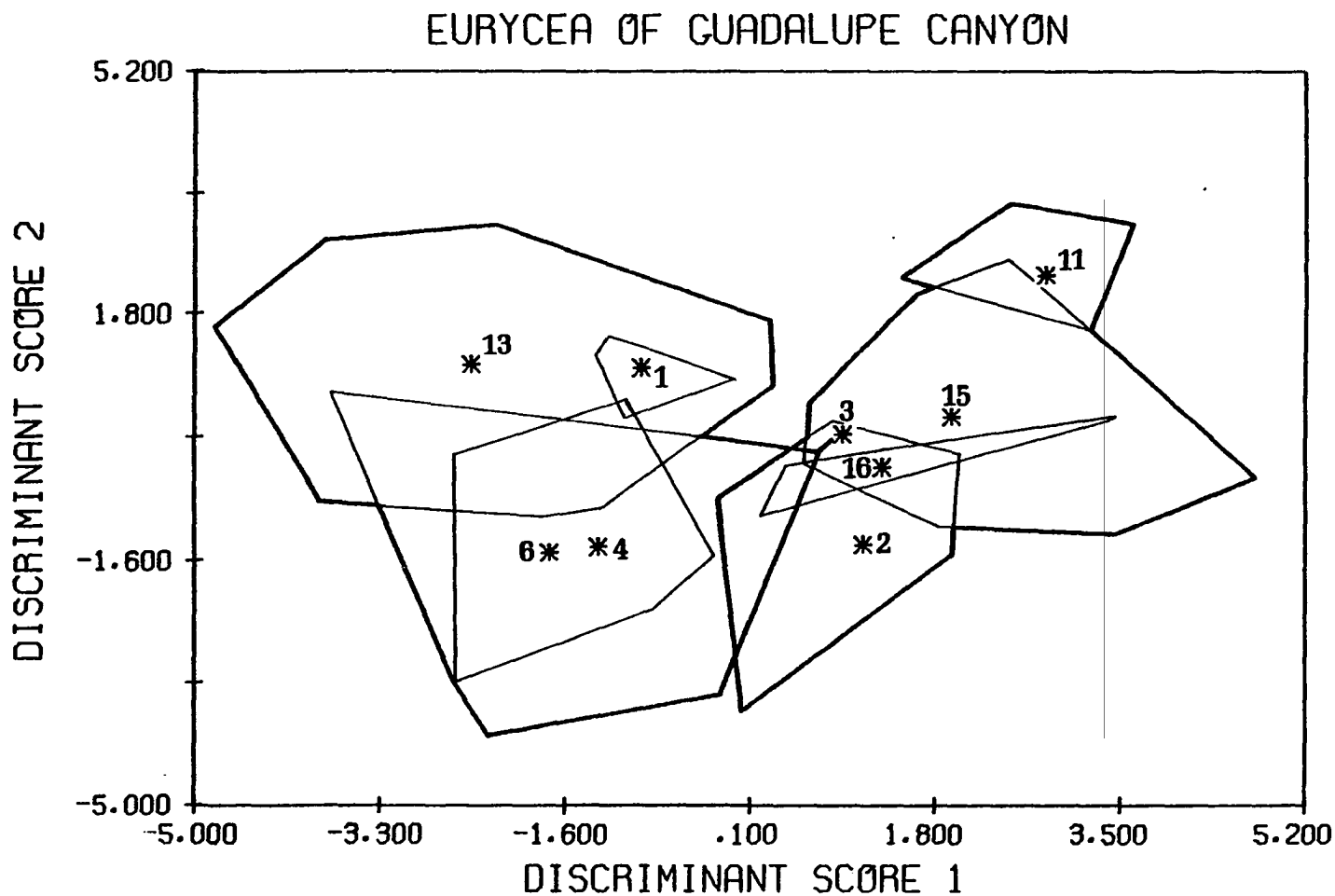

epigean specimen is misclassified as a troglobite, and only 4 troglobites (from sites 3, 6 [2 specimens] and 13) are incorrectly assigned to the epigean group.

From an inspection of Figure 33 it is clear that the epigean and troglobitic subgroups exist in discriminant space. Group membership is unrelated to the location of sites along the river. Within the epigean subgroup the relative positions of three of the four populations correspond exactly with the frequency of occurrence of individuals in the cave environment. The sample from Victor Phillip Water Cave (site 2) bridges the epigean and troglobitic subgroups and is the only population in which specimens are frequently found in the cave as well as on the surface. Rebbecca Creek Spring (site 16) issues from a small cave, of which only a few meters are accessible owing to an artificial dam at the entrance. One salamander was seen, but not collected, above this dam on one of three visits. Puter Creek spring (site 15), where no cave is evident, issues from gravel in a streambed at the Hensel-Glen Rose contact; the sample from this site has relatively high values on both discriminant axes, exceeded only by the Honey Creek Cave E. neotenes. The Honey Creek population seems at first sight to contradict this trend. It is the most distinct of the epigean populations, yet the spring in which it occurs emerges directly from a large cave, and one specimen was collected about 25 m inside the entrance (Mitchell and Reddell, 1965). When these findings are placed in conjunction with the know-

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ledge that E. tridentifera occupies Honey Creek Cave the apparent anomaly can be reversed by accepting the interpretation that competitive exclusion of E. neotenes by E. tridentifera has taken place. My interpretation is that E. neotenes fails to show the expected moderate degree of troglobitic adaptation owing to selection against individuals in the subterranean adaptive zone, where a different, highly specialized troglobitic population is established. These data might be further interpreted as indicating character displacement, if only local populations of E. neotenes are considered. A broader view suggests that this is not the case, in that neither of these sympatric populations differs in a substantive way from other populations of their respective taxa.

The sequence of colonization in Honey Creek Cave is unclear. Distributional evidence suggests that E. tridentifera has entered the Guadalupe region from the Cibolo sinkhole plain to the south, where the majority of populations occur, whereas E. neotenes has probably long occupied this area. The development of cave systems probably began prior to the entrenchment of the Guadalupe River, as is presently the case along Cibolo Creek, but three lines of evidence suggest that large regional cave systems such as occur to the south did not form during this period. Unlike the Cibolo system, the middle Guadalupe drainage is distant from the Balcones Fault Zone aquifer. In the absence of the strong hydrologic gradient this proximity provides, the

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movement of groundwater through developing cave systems was probably slow prior to the entrenchment of the river, at which time a strong potential gradient developed. A low groundwater divide presently exists between the Guadalupe and Cibolo drainages (George, 1952; Reeves, 1967), and there is no evidence that any of the caves of the Guadalupe region are tributaries of the Cibolo system. The size and form of the Guadalupe caves provides a second point of evidence. Most are relatively small, and none is known to be connected, as might be expected if a large regional system had been transected by the developing river canyon. Two caves (sites 7 and 11) bifurcate near their present entrances, and both passages are approximately equal in size. These distributaries did not develop until the cave was breached by erosion, and their equal sizes suggest that the caves which existed prior to entrenchment were small (W.H. Russell, personal communication, 1974). The third point is simply that E. tridentifera occupies only one of the Guadalupe caves, contrary to an expected broader distribution if regional systems were developed.

Populations of E. neotenes probably occupied the developing springs at a relatively early date, perhaps prior to the arrival of E. tridentifera, but there is little evidence to indicate when colonization of caves by epigean populations began. This process is apparently still occurring, both in the Guadalupe region and elsewhere on the Edwards Plateau (Sweet, 1977a [Chapter V]). It is parsimonious to assume

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that E. tridentifera antedates the events which would lead to colonization of Honey Creek Cave by E. neotenes, rather than proposing a more complex model involving the extirpation or exclusion of an existing troglobitic population of E. neotenes.

In summary, I interpret these data as indicating that E. neotenes has been excluded from the cave environment by E. tridentifera. In all other localities in the Guadalupe canyon E. neotenes inhabits accessible caves, and is frequently wholly troglobitic. Throughout the Guadalupe canyon initially epigean populations of E. neotenes have colonized or are colonizing available caves, save in the one case in which the cave is occupied by a highly specialized troglobitic congener. Discriminant analyses indicate the existence of a morphological trend in populations of E. neotenes in the Guadalupe canyon; predominantly troglobitic and predominantly epigean populations are distinct but linked through a population which frequents both environments. Further, the Honey Creek Cave E. neotenes are the most distinctive of the epigean populations.

There may be evidence of competitive displacement in the overall pattern of distribution of E. neotenes and E. tridentifera as well as in the local situation at Honey Creek Cave. Each of the instances of secondary contact demonstrated or inferred here is peripheral to the distribution of E. tridentifera; the latter is enclosed within the range of E. neotenes. Surface dwelling populations of the latter

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are uncommon within the region occupied by E. tridentifera, probably because the geologic conditions producing extensive subterranean drainages generally preclude the existence of reliable springs. Troglobitic populations of E. neotenes are apparently absent from the main range of E. tridentifera on the Cibolo sinkhole plain. This is the only well-surveyed cave region in the range of E. neotenes lacking such populations, a distinction suggesting that the presence of the advanced troglobite has prevented subsequent colonization on a regional scale.

Conclusion

While each of the three samples considered here can be distinguished from the remaining popoulations of the Texas Eurycea on grounds which suggest the occurrence of hybridization, the strength of this evidence varies among cases. Hybrid origin is very likely for the Honey Creek Cave sample: all examined criteria agree, and the presumed parental populations occur in sympatry. The criteria are also fully met in E. troglodytes, though specimens which are clearly referable to either of the presumed parental taxa have not been found in Valdina Farms Sinkhole. The weight of evidence nonetheless favors the interpretation that this population is a hybrid swarm of temporally unstable composition, in which the genetic influence of E. neotenes presently predominates. The presently available evidence is insufficient to evaluate conclusively the status of E. lati-

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tans, though an unusual degree of individual heterogeneity exists in the population, especially in numbers of trunk vertebrae. Its proximity to the known range of E. tridentifera lends some plausibility to the conclusion that E. latitans represents a troglobitic population similar to E. neotenes, but influenced by hybridization with E. tridentifera.

A series of systematic questions is raised in viewing these samples as instances of hybridization. If such an interpretation is accepted, the apparent distinctiveness of E. neotenes and E. tridentifera must be examined closely, as the degree of reproductive isolation between these largely allopatric forms appears to be rather slight despite the existence of considerable morphological and ecological differences.

A degree of reproductive isolation appears to be in effect at Honey Creek Cave; this may result from either the existence of isolating mechanisms, or very infrequent contact of the two populations across the gradient separating cave from surface habitats. While the latter distinction is of great importance in explaining the presence of E. neotenes, it seems unlikely that habitat preferences alone would be effective in isolating the two genomes over an extended period. These populations would be expected to be competitively superior in their respective habitats (see, for example, Poulson and White, 1969), empowering selection against hybridization and hence for the origin of reproduc-

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tive isolation. The comparatively low concordance value of Honey Creek Cave E. tridentifera may reflect the movement of hybrid individuals into the population in the past, but on the whole these populations remain distinct.

Eurycea troglodytes occurs about 75 km WSW of the westernmost records for E. tridentifera in the Cibolo sinkhole plain and the fault-zone aquifer of central Bexar County (Fig. 23). Beyond the inference from the data presented above, little evidence exists on whether populations of E. tridentifera or a similar form may occur in the intervening region. While hydrologic evidence indicates that the central region of the fault-zone aquifer behaves as a unit on a broad scale (Petitt and George, 1956; Garza, 1962, 1966; Maclay, 1974), local hydrology is quite complex in the intensely faulted and fractured strata of the Balcones Fault Zone, and no simple interpretation can be made. Sampling of aquatic troglobites in the central region of the fault-zone aquifer is difficult, as the structural complexity of this region contributes to a paucity of caves in which the water table is accessible. Despite an extensive survey program on the cave fauna of the Edwards Plateau, no records of aquatic troglobites of any kind are known in the region between Valdina Farms Sinkhole and the range of E. tridentifera (Reddell, 1965, 1970). The existing faunal evidence is equivocal. Ostracods of the genus Candona and the isopod genera Cirolanides and Conasellus occur in Valdina Farms Sinkhole and elsewhere on the eastern limb of the Edwards

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Plateau, but are not reported from caves inhabited by E. tridentifera. Conversely, species of the planarian genus Sphalloplana and the amphipod Stygonectes occur as far south in the Edwards Plateau as the range of E. tridentifera but are not reported from the Valdina Farms Sinkhole region (Mitchell and Reddell, 1971). These faunal contrasts might be taken as evidence of limited hydrologic continuity between the two areas, but because they represent negative evidence in a relatively poorly sampled area, this interpretation is questionable. Advanced troglobitic Eurycea might reach the Valdina Farms Sinkhole region via the main fault-zone aquifer, or by way of groundwater conduits associated with the Woodward Fault, which extends from the range of E. troglodytes to within a few kilometers of the Cibolo sinkhole plain.

I interpret E. troglodytes to be a hybrid swarm resulting from the incorporation of occasional individuals of E. tridentifera into a larger population of E. neotenes, which may be either a resident troglobite or composed of individuals washed into the cave system from local surface populations. Reproductive isolation is unlikely to arise under these conditions owing to both the scarcity of E. tridentifera and the lack of appreciable heterogeneity in the local environment which might permit the coexistence of troglobitic populations of different degrees of specialization. The rarity of E. tridentifera presumably prevents competitive esclusion of the less specialized population of E. neotenes.

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The persistence of E. latitans in caves of the Cibolo Sinkhole plain adjacent to the main range of E. tridentifera suggests the existence of a barrier preventing extensive contact between the two populations. Free contact would presumably result in either the formation of a hybrid swarm or the exclusion of E. latitans by its more highly specialized troglobitic congener, as has apparently occurred elsewhere (involving E. neotenes) on the Edwards Plateau. Significant physical barriers seem to be lacking among the drainages of the Cibolo sinkhole plain on the basis of regional stratigraphic and structural uniformity (Stricklin, Smith and Lozo, 1971), and on the uniform hydrologic behavior of the caves during floods on Cibolo Creek (personal observations, 1971, 1973, 1974). I have previously suggested (Sweet, 1976) a potential biological barrier to the westward dispersal of E. tridentifera based on the presence of fish in the caves of this area and differences in the escape behavior of intermediate and advanced troglobitic salamanders; this hypothesis is reviewed and expanded below.

Several caves in the Guadalupe canyon and along Cibolo Creek regularly contain a variety of fishes introduced during periods of flooding (Reddell, 1967b, 1971; and personal observations). These fish apparently survive for appreciable periods, and include such potentially predatory genera as Ictalurus, Lepomis and Micropterus; however, there is presently no direct evidence that troglobitic Eurycea are consumed in these situations. Nonetheless, with the excep-

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tion of the Cascade Caverns-Cascade Sinkhole system (site 2 of Fig. 23), caves with fish are without populations of Eurycea, though some (such as Prassell Ranch Cave and Spring Creek Cave in the Guadalupe canyon, sites 5 and 7 of Fig. 31) are apparently otherwise suitable, and are bracketted by fish-free caves inhabited by Eurycea (Fig. 31). Eurycea latitans coexists with Lepomis spp., including L. cyanellus, and Micropterus spp. in Cascade Sinkhole. Most of the salamanders occur in pools too small to support fish, but a few have been observed in piles of cobble and plant debris in the larger pools (A.G. Grubbs, personal communication, 1976). The Cascade system appears to contain more deposits of gravel and cobble than other caves in the region, which may permit the persistence of Eurycea in the presence of fish.

Incidental observations of escape behavior indicate that E. tridentifera may be more susceptible to predation by fish than are the less specialized troglobites. Individuals of E. neotenes, E. latitans and E. troglodytes swim rapidly away when disturbed by an observer without rising from the substrate and frequently seek to burrow beneath objects which they contact. By contrast, individuals of E. tridentifera generally swim upward for a short distance, slow, and drift back to the substrate with limbs extended (Bogart, 1967; and personal observation); no instances of burrowing have been noted. It is my impression that E. tridentifera seems to swim less rapidly, less far, and less directly away from a disturbance than do individuals of other populations.

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These attributes would seem to facilitate predation by fish, even in a lightless environment; if so, these observations may explain the minimal intrusion of E. tridentifera into the caves of the western Cibolo plain. Fish do not seem to occur in cave systems more than about one-half kilometer distant from the creek bed, though this may simply reflect the fact that the lower levels of these caves remain unexplored. The upper passages typically lack extensive pools, and most terminate in 10-20 m waterfall pits. Evidence suggesting the dispersal of E. latitans into the main sinkhole plain is slight; several unconfirmed reports of salamanders in caves near the Cascade system may represent extensions of this population.

In conclusion, I suggest that the observed interactions are consistent with the interpretation that E. neotenes and E. tridentifera are closely related but distinct species. Eurycea troglodytes Baker, 1957, consists of a hybrid swarm and is thus an invalid taxon which is here placed in the synonymy of E. neotenes Bishop and Wright, 1937 (part) and E. tridentifera Mitchell and Reddell, 1965 (part). Continued recognition of E. latitans is probably unwarranted, as its distinctive characteristics could easily result from limited hybridization. Were it not for the extreme variation observed in vertebral number this population would be morphologically indistinguishable from most of the independent and parallel troglobitic populations of E. neotenes which occur widely on the Edwards Plateau. Accordingly, I

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suggest that the name E. latitans Smith and Potter, 1946, be regarded as a junior synonym of E. neotenes Bishop and Wright, 1937 (see also Chapter IV).

Summary

Three samples of paedogenetic salamanders of the genus Eurycea of the Edwards Plateau of central Texas show unusual levels of variation in comparison to 132 other populations examined in the course of a more comprehensive study. Correlation, discriminant and concordance analyses of proportional and meristic characters suggest that these samples consist of or include hybrids between the widespread epigean and troglobitic E. neotenes and the highly specialized troglobite E. tridentifera. The two species are sympatric in one case, contiguously allopatric in a second, and widely separated in the third. Parapatry is the rule in the overall distribution of troglobitic E. neotenes and E. tridentifera. Partial reproductive isolation has apparently arisen in sympatry at Honey Creek Cave, Comal County, but not elsewhere; the interaction between these populations may represent a case of competitive exclusion. Eurycea tridentifera occurs in caves adjacent to those inhabited by E. latitans in Kendall County, but contact between the two populations appears to be infrequent. This separation in a geologically homogeneous area may be the result of differences in the abilities of these two populations to coexist with fish. Eurycea troglodytes of Valdina Farms Sinkhole, Medina County,

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appears to be a hybrid swarm of temporally unstable composition, in which parental phenotypes are uncommon or lacking.

These interactions are held to validate continued recognition of E. neotenes and E. tridentifera, but require suppression of the name E. troglodytes as an invalid taxon. The status of E. latitans as distinct from E. neotenes is questioned; as its diagnostic characteristics appear to arise from infrequent hybridization with E. tridentifera the name E. latitans is considered a junior synonym of E. neotenes.

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I have again benefitted from discussions with William

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CHAPTER VII

ON THE STATUS OF *EURYCEA PTEROPHILA* (AMPHIBIA: PLETHODONTIDAE)

Introduction

Names applied to questionable taxa with restricted geographic distributions or of rare occurrence tend to have considerable inertia in the literature, and often persist without reevaluation well beyond the emergence of a general consensus on their validity, primarily as a result of the scarcity of preserved material. Exclusively allopatric taxa compound this problem, in that series representative of the range of variation in related populations must be at hand before meaningful evaluation of the taxonomic status of a described form can take place. Most of these problem criteria are met by the paedogenetic plethodontid salamanders of the Edwards Plateau of central Texas. The Fern Bank salamander, *Eurycea pterophila* Burger, Smith and Potter (Burger *et al*., 1950) has generally been accorded species status by workers with some familiarity with the diversity of the Texas *Eurycea* (Baker, 1957, 1961; Blair, 1957; Potter and Rabb, 1960; Mitchell and Reddell, 1965; Wake, 1966; Bogart, 1967; Mitchell and Smith, 1972), though there have long been serious doubts about its validity. With increasing frequency authors have relegated *E. pterophila* to subspecific status within *Eurycea neotenes* (e.g., Schmidt, 1953; Conant, 1958, 1975; Brame, 1967; Raun and Gehlbach, 1972; Hamilton, 1973), but only Brown (1967) has

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published a brief statement in justification for this course of action. Hendricks (1973) is the first author to suggest that E. pterophila should be denied nomenclatural status; the taxon is not listed in a recent checklist by Thomas (1974), and is the only named form of Eurycea of restricted distribution not protected as rare or endangered by Texas state law. The trend away from recognition of E. pterophila in recent herpetological literature is clear, but there remains scant evidence for this conclusion.

Eurycea pterophila is known from a single small spring on the south bank of the Blanco River, 8.3 airline km E (not NE as stated in the type description and in subsequent literature) of Wimberley, Hays County, Texas. The population occupies an area of shallow travertine pools on a shaded slope below the bluff from which Fern Bank Spring (locally long known as Little Arkansas Spring) emerges. This habitat is estimated to comprise ~ 230 m^2 (Burger et al., 1950), and the population of salamanders has been estimated to be rather small (Conrads, 1969). This population has been repeatedly and severely disturbed by collectors, with the result that 200 specimens are available in public collections. Numerous additional individuals from this site have been utilized in a variety of experimental contexts (Andrews, 1962; Norris et al., 1963; Bogart, 1967; Barrett and Benjamin, 1977), most without finding their way into collections.

No account has reexamined the characters on which Bur-

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ger et al. (1950) established E. pterophila, and no further characters of diagnostic value have emerged from the work mentioned above. Burger et al. (1950) indicated that E. pterophila was indistinguishable from E. neotenes in external morphology, but could be characterized on the basis of "irregular" reductions in the phalangeal formula (Table 1, p. 53), in the proportions of the sacral and presacral ribs, and in the form of the urohyal element of the hyobranchial apparatus. Specifically, the sacral rib of E. pterophila was stated to have a single articulation with the sacral vertebra, contrasting with double articulations in Eurycea nana, E. neotenes and Eurycea latitans. The presacral rib of E. pterophila was maintained to have a dorsal head (tuberculum) of about half of the length of the ventral head (capitulum), but less than the length of the rib; the presacral rib heads were stated to be of equal length in other species of Texas Eurycea. An irregularly Y-shaped posterior basibranchium (=urohyal) was contrasted with the absence of this element in topotypic E. neotenes, its irregular rounded form in E. nana, and a triradiate form in E. latitans.

The present paper documents the widespread occurrence of features presumed diagnostic of E. pterophila in populations of E. neotenes and other Texas Eurycea, and the degree of contradiction in these characters shown in a series of topotypes. This evidence suggests that E. pterophila be synonymized with E. neotenes.

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Material

This work is based on ~4500 specimens of Texas *Eurycea*, including 97 specimens of *E. pterophila*. Because all of the stated diagnostic features of this form are skeletal, emphasis has devolved to data obtained from radiographs and cleared and stained specimens. Although radiographs of all *E. pterophila* on hand have been available, not all could be fully analyzed owing to inappropriate position or the lack of sufficient ossification in juvenile specimens. I examined 33 cleared and stained topotypic specimens of *E. pterophila*, and compared them with: 59 cleared and stained *E. neotenes* (representing the type locality and 10 others); 40 *E. nana*; and a number of specimens from the several troglobitic populations of the Texas *Eurycea*, as well as five cleared and stained *Typhlomolge rathbuni*. Cleared and stained specimens of *E. pterophila*, *E. neotenes* and *E. nana* are identified and their repositories indicated in Appendix .

Regrettably, the type series of *E. pterophila* is in a private collection, and has not been available for examination. The location of the type locality is well known, however, and it is certain that all *E. pterophila* I examined are from that site.

Results

Phalangeal Reduction

From Table 1 of Burger *et al*. (1950: p. 53) it is evident that their term "phalanges" includes the metapodial

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elements as well as phalanges; the term is herein employed in its usual sense. The Texas Eurycea have phalangeal formulae of 1-2-3-2 (forelimb) and 1-2-3-3-2 or 1-2-3-3-1 (hindlimb). Inspection of Fig. 34 suggests that the phalangeal reductions observed in E. pterophila are primarily pathological in nature, involving the loss of terminal phalanges or whole digits long after their differentiation and growth, rather than some regular pattern of reduction in phalangeal formula as is frequently seen in other tetrapods. The lack of anatomical modification of the tips of the reduced digits and their frequent protrusion from the skin, together with the frequent presence of proximal fragments of the missing phalanges strongly suggests that these elements were lost by action of mechanical injury or disease subsequent to the development of a normal phalangeal complement. Further evidence for this view may be adduced from the frequent occurrence of regenerating digits of normal and abnormal morphology (Fig. 34). Although difficult to document in a definitive fashion, the location and structure of the digital deformities bear close resemblance to the effects of redleg (Aeromonas sp.) infection (Reichenbach-Klinke and Elkan, 1965). This disease in Eurycea results in part in localized necrosis which often removes only parts of bony elements; subsequent regeneration is more frequently abnormal than is regeneration from mechanical injury.

Redleg has been reported in natural populations of E. neotenes (Hunsaker and Potter, 1960), and the reasonable

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Figure 34. Hind feet of 5 specimens of Eurycea pterophila, drawn from cleared and stained specimens. Cartilage is stippled; a,b,c, and e represent left feet. The figure shows; (a) normal tarsal, metatarsal and phalangeal complement (MVZ 120936); (b) digits deformed by mechanical injury or disease; note protruding and broken phalanges, and the absence of appropriate terminal structure in digits 1, 2 and 4 (MVZ 120925); (c) (TCWC CS-121) and (d) (MVZ 120924), regenerating digits of abnormal structure; note fusion of tarsals 4 and 5 in (d); (e) example of normal reduction of phalangeal number in digit 5 (MVZ-DBW 232).

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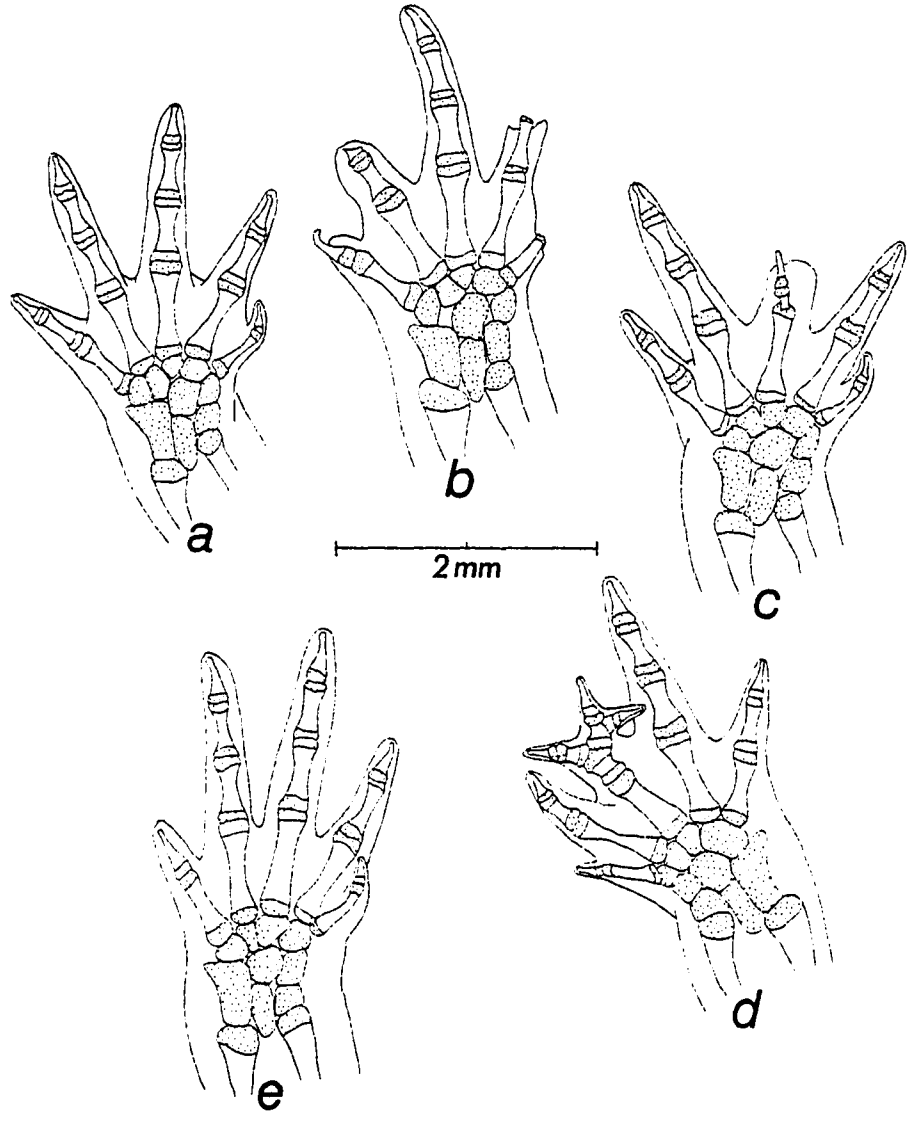

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suggestion has been made that the disease is transmitted between isolated springs by dispersing leopard frogs (Rana berlandieri). I have found salamanders with the symptoms of this disease in the field in four populations of E. neotenes distributed in three western drainages of the Edwards Plateau (Cypress Creek, Frio drainage; Ash Hollow and Mill Creek, Sabinal drainage; and in the upper tributaries of the Seco Creek drainage), in addition to the report noted above from Helotes Creek, in the Medina drainage. Patterns of digital deformity similar to those seen in E. pterophila occur in some specimens from these areas, and the condition is occasionally noted in a variety of other populations. Animals contracting redleg in the laboratory generally show the first signs of infection on the feet and the dorsal tail fin, and the infected digits are invariably lost prior to the death or recovery of the salamander.

A fundamental developmental reorganization of the foot in ontogeny, or any other genetically based mechanism should be evident in equal or greater frequencies in juveniles than in adults, whereas the effects of injury or disease should be cumulative with size and presumed age, and thus more frequent in adults than in juveniles. Reference to Fig. 35 demonstrates that few small E. pterophila show foot deformities, and that among those larger individuals with deformities the number of deformed digits tends to increase with size and presumed age. These lines of evidence strongly indicate that the observed pattern of phalangeal loss in E. pterophila

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Figure 35. Relationship of the total number of deformed digits per specimen to body size in *Eurycea pterophila* showing the tendency for deformations to be more frequent in large specimens consistent with the hypothesis of environmental causality.

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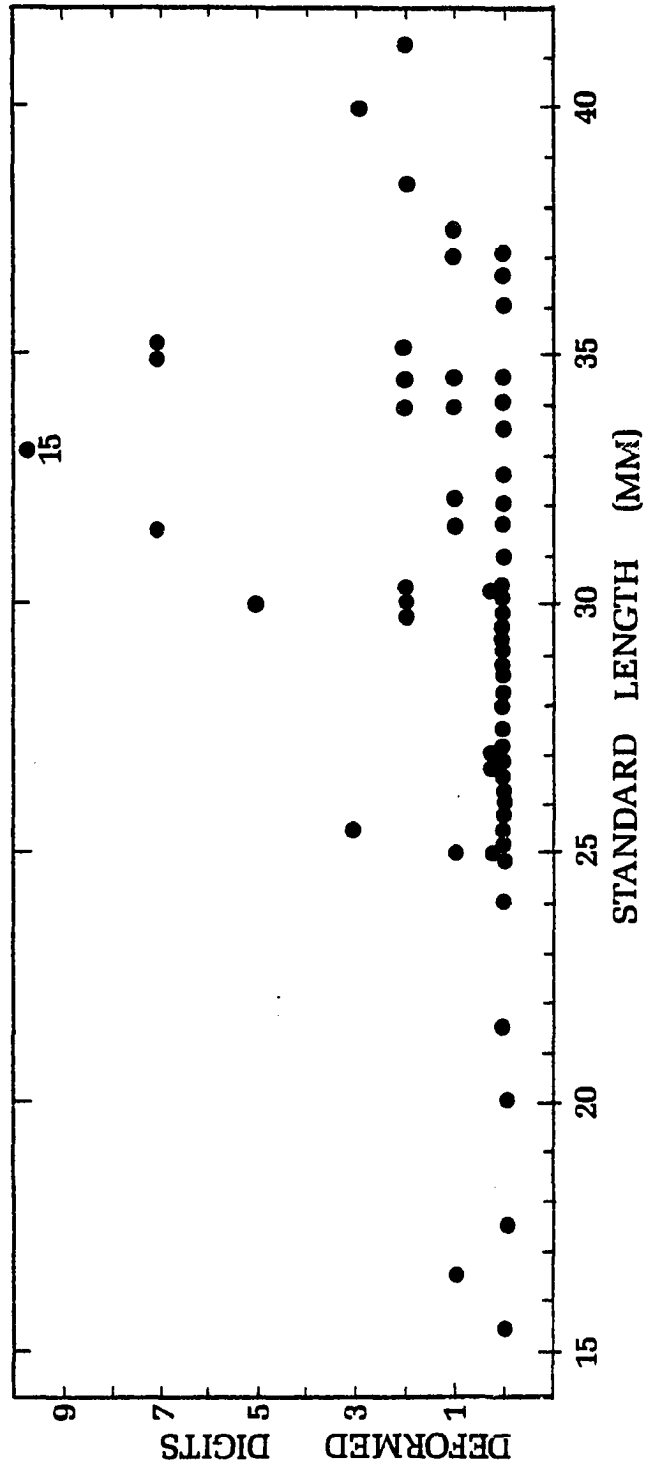

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is wholly phenotypic, and hence is without value as a diagnostic character.

A tendency to reduce the number of phalanges in the fifth digit from two to one is expressed in several families of salamanders (Dunn, 1926). This reduction is occasionally noted in specimens of Texas Eurycea. In such cases, the remaining terminal phalanx is appropriately shaped, rather than retaining traces of a distal articular facet as seen in the deformities previously discussed. In E. pterophila nine of 70 specimens examined show bilateral reduction to a single phalanx on the fifth digit; this number may be somewhat higher, considering the fact that four of the 70 animals had entirely lost their fifth digits to injury or disease. This frequency is greater than in most populations of E. neotenes; in a brief survey of radiographs, I find at least one individual showing phalangeal reduction in the fifth digit in 10 of 25 populations of E. neotenes. The wide occurrence of this reduction, and its low expression in the Fern Bank Spring population do not appear to constitute grounds for nomenclatural distinction.

Sacral and Presacral Ribs

The proportions of the sacral and presacral ribs are variable in the Texas Eurycea both in ontogeny and among populations. The "presacral" ribs figured by Burger et al. (1950, Plate VI) apparently include the sacral rib as well, denoted as "presacral #1"; statements in the text in refer-

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ence to the last rib also pertain to the sacral rib, and their "penultimate rib" is thus that of the presacral vertebra. As far as can be determined from the available cleared and stained ontogenetic series of E. nana and E. neotenes the pattern of rib development in the Texas Eurycea is similar to that described for Eurycea bislineata by Wake and Lawson (1973). The ventral rib head ossifies prior to the appearance of ossification in the dorsal head; the dorsal head is not preformed in cartilage on the posterior trunk vertebrae, but does so appear in the sacral rib. The dorsal head of the sacral and presacral ribs ossifies from the shaft dorsomedially to join the dorsal rib bearer. This process is comparatively rapid in the sacral rib, which is bicipital in E. pterophila as small as 25 mm in standard length. The dorsal head of the presacral rib ossifies more slowly or not at all, remaining unicipital in some cases.

The sacral rib is stated to be unicipital in E. pterophila. Examination of the figures provided (Burger et al., 1950, Plate VI, D and E) shows the sacral rib in these specimens to have both heads, which are simply fused together by bony growth in the interhead region, rather than being truly unicipital. In 27 cleared and stained E. pterophila both fully bicipital and fused bicipital conditions occur: categorization of this variation is difficult, and asymmetry is common. Of 54 sacral ribs examined, 29 are strongly bicipital (heads separated by a gap at least as deep as either head is wide), and 14 are fully fused (with no interhead

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concavity); the remainder are of intermediate form. The morphology of the articulation of the sacral rib is thus not a constant character as represented in E. pterophila. As is the case within the topotypic series, sacral rib form is quite variable in and among other populations of the Texas Eurycea. The most frequent pattern consists of predominantly bicipital ribs, with occasional secondary fusions as seen in E. pterophila. Some populations show near constancy in sacral rib form, as follows. All examined specimens (seven) from Henderson Branch Creek, Kerr County, have fused rib heads, as do the specimens (three) from Salamander Cave, Travis County. The sacral rib is bicipital in all 16 specimens from Mill Creek, Bandera County. In the remaining populations examined, including topotypic E. neotenes and specimens from five other localities, as well as in E. nana, E. latitans, Eurycea troglodytes and Eurycea tridentifera, most sacral ribs are bicipital, but all populations show the fused condition in at least one individual. Accordingly, by virtue of variation in the topotypic population and corresponding variation in all other species of Texas Eurycea, the morphology of the sacral rib is judged to be an inadequate character on which to differentiate the Fern Bank Spring population.

The form of the presacral rib is likewise highly variable in E. pterophila and in other Texas Eurycea. Part of this variation is ontogenetic, but there is much additional individual variability. In 28 cleared and stained E. pter-

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ophila the presacral ribs are: unicipital in six specimens (15.5-33.5 mm standard length, $\bar{x}$ 28.3 mm); developing a dorsal rib head but not fully bicipital in 11 specimens (25.0-37.4 mm standard length, $\bar{x}$ 30.8 mm); and fully bicipital in 11 specimens (25.5-41.4 mm standard length, $\bar{x}$ 34.1 mm). The ratio of dorsal to ventral rib head length held to be diagnostic of E. pterophila is in fact an ontogenetic variable which ranges from zero to one in topotypes. There is considerable interpopulational variation in the degree of development of the ossified presacral rib. It is absent in most specimens from Henderson Branch Creek, invariably small and fused with the transverse processes in Salamander Cave specimens, and nearly always unicipital in E. nana and in topotypic E. tridentifera (but becoming bicipital in other populations of this species which reach larger adult size). Other populations of E. neotenes generally show the ontogenetic progression from unicipital to bicipital presacral ribs.

Urohyal Form and Ossification

There are several errors in the representation of the hyobranchial apparatus of species of Texas Eurycea figured by Burger et al. (1950, Plate VII), the most significant for this discussion being two: the failure to show the cartilaginous stylus which connects the urohyal to the remainder of the hyobranchial apparatus; and the failure to illustrate the form of the cartilaginous processes of the urohyal pos-

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terior to the illustrated ossification centers. The urohyal is continuous with the hyobranchial apparatus proper in all larval hemidactyliine plethodontids (Wake, 1966), and the cartilaginous anlage of the urohyal is triradiate (with occasional exceptions) in all, though it is variably mineralized or ossified. The urohyal and its stylus are preformed in cartilage early in larval life; the lateral rami of the urohyal provide an insertion site for the rectus cervicis superficialis and hebosteoypsiloideus musculature from the ventral surface of the unit. The median ramus lies in the midventral raphe, where it is continuous with the connective tissues of the linea alba. The degree of ossification of the urohyal is size related, and is consistent with a stress response to the mechanics of gape-and-suck feeding; the lateral rami generally are bridged by bone across the body of the element in an irregularly Y-shaped configuration prior to the ossification of the median ramus.

The cartilaginous urohyal of E. pterophila is triradiate in 18 of 24 cleared and stained specimens in which the structure can be clearly seen, and is clearly biradiate in five. In this same series the ossified urohyal can be interpreted as being irregularly Y-shaped in seven of 24 specimens, is distinctly triradiate in two, and is of irregular outline in nine; the element is not ossified in six specimens $<$ 32 mm in standard length.

The form of the urohyal shows considerable ontogenetic, individual, and interpopulational variation in the Texas

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Eurycea. It is uniformly triradiate either in cartilage or when ossified in the following populations of E. neotenes: Mill Creek (16 specimens); Fessenden Branch (three specimens); Lambs Creek (three specimens); Henderson Branch (seven specimens); Cypress Creek (two specimens); East Frio River (one specimen); and 15 miles (=24 km) N of Leakey (one specimen). The urohyal is also present, ossified, and triradiate in topotypic E. neotenes larger than about 30 mm standard length, and in E. nana larger than about 28 mm standard length, contrary to the statements of Burger et al. (1950). Larger individuals of troglobitic populations of E. neotenes, and of E. latitans, E. troglodytes, E. tridentifera, and Typhlomolge rathbuni also display triradiate bony urohyals. In most of these populations the ossified urohyal passes through a biradiate ontogenetic stage. On the basis of the observed variability in topotypic E. pterophila and in other populations of all recognized taxa of the Texas paedogenetic assemblage, conformity to the general hemidactyliine urohyal morphology is good. The form of the ossified urohyal is not a character of merit in the Fern Bank Spring population.

Conclusion

The characters used to diagnose E. pterophila are representative of no more than a minority of individuals in the topotypic population; further, they represent either ontogenetic stages or environmental effects. Rib and hyo-

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branchial characters are shared by individuals of all named taxa of the Eurycea of the Edwards Plateau of central Texas, and foot deformities equivalent to those seen in E. pterophila occur widely in E. neotenes. No additional characters have been noted in the course of this work which would tend to substantiate nomenclatural standing for the Fern Bank Spring population, or to group it with any subset of the populations of E. neotenes, either in the adjacent region or across the known range of surface populations. Accordingly I recommend that Eurycea pterophila Burger, Smith and Potter, 1950 be considered a junior synonym of Eurycea neotenes Bishop and Wright, 1937, without subspecific status. Eurycea neotenes is a widespread and locally abundant form of sufficient morphological diversity that the inclusion of the Fern Bank Spring population requires no modification in its diagnosis.

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CHAPTER VIII

CONCLUSION:

THE DEVELOPMENT OF DIVERSITY IN THE TEXAS *EURYCEA*

The evolutionary development of the Texas *Eurycea* has been strongly influenced by regional geology and geomorphologic processes. These salamanders now persist in an otherwise unfavorable environment only because of the existence of reliable springs; the origin of paedogenesis, the impetus for the colonization of caves and the basis for the extensive occurrence of parallel evolution are all correlates of the presence and geologic evolution of springs on the Edwards Plateau.

The ancestors of the present radiation of the Texas *Eurycea* probably reached the Edwards Plateau during the Miocene (Wake, 1966) by way of the Interior Highlands, where their closest relatives now occur. The Edwards Plateau was exposed as a structural uplift prior to the Miocene, for by that time its blanket of Gulf Series rocks had been stripped away to expose the resistant Edwards Group limestones which form much of its present surface. Middle Miocene deltaic deposits along the Texas coast conclusively demonstrate the erosion of Segovia Formation limestones on the Edwards Plateau, and hydrologic evidence is strong that the aquifer associated with the Balcones Fault Zone began its development at this time (Abbott, 1975).

The distributional connection between the Interior

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Highlands and the Edwards Plateau was probably a tenuous and fragile link for the ancestral populations of Eurycea, whose descendants are now associated with gravelly springs and streams. Most of the intervening region has been flat-lying since the middle Tertiary, resulting in low stream gradients and a concomitant presence of silty rather than gravelly beds. The land surface of northeastern Texas does not provide local sources of gravel, and low-gradient streams are incompetent to transport large clastics from distant source areas. It thus seems likely that the distributional connection between the Interior Highlands and central Texas was a short-lived feature.

The topography of the eastern Edwards Plateau in the Miocene probably resembled that of the current west-central drainages, with deep, narrow canyons and sharp, highly-dissected divides maximizing the maintenance of relatively mesic conditions along the coastal margin of the plateau. Populations ancestral to the present species may have been continuously distributed from the eastern terminus of the Balcones Fault Zone south and west through the marginal plateau drainges to the vicinity of the Devils River. These animals were in all likelihood closely similar to the metamorphosing populations of Eurycea neotenes occurring today as relicts within a relictual assemblage.

It seems reasonable to assume that these ancestral Eurycea brought with them a biphasic life cycle which was maintained for a period on the plateau. Paedogenesis seems

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to have arisen at the time that regional climatic changes reduced the distribution of mesic habitats to canyons in the immediate vicinity of springs; this process presumably occurred at a rate partially dependent on local conditions. Metamorphosis now persists as a life-history strategy in a few sheltered populations in the most highly-dissected divide region of the plateau, having been replaced by paedogenesis elsewhere in the range of the Texas Eurycea. Both paedogenetic and metamorphosed individuals of Eurycea neotenes are aquatic, though the latter appear to feed terrestially, and both are closely restricted to the immediate vicinity of springs. These sites represent the most temporally reliable and thermally stable epigean aquatic environments on the plateau.

Despite their stability in the short term, springs are susceptible to droughts, and are geologically evanescent structures. Flow is reduced or may cease altogether during dry periods, further restricting the areal extent of habitat suitable for salamanders, and frequently requiring them to become interstitial or to spend periods underground in spring channels. Metamorphosed individuals are at a selective disadvantage as visually-orienting and tongue-feeding animals under these conditions; paedogenesis thus represents an adaptation for survival during times of drought. That some epigean populations are presently obliged to spend dry periods beneath the surface is documented by records obtained in the course of this work.

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The occurrence of springs at several stratigraphic levels in the rocks of the plateau, and the variation in their locations with respect to potential catchment and storage areas for groundwater, result in a range in temporal reliability for springs. Those in headwater canyons receive groundwater from a large recharge and storage area, and are highly reliable in flow; others situated below narrow divides or on erosionally-levelled terrain have small recharge potentials, and are episodic in flow. A simple hydrologic model based on the estimation of potential recharge areas is effective in describing the observed pattern of presence or absence of populations of Eurycea neotenes in springs, and can be extended to a predictive level. On this basis, a survey of the mapped springs of the southern half of the Edwards Plateau suggests that 1600-2400 populations of Eurycea neotenes may presently exist, and that their actual distribution is not much different from that now documented. Populations are predicted to occur beyond the documented range only in northern Gillespie County.

As springs fail through erosion of the land surface and the resultant lowering of the local water table, resident populations must either spend increasing amounts of time underground or disappear. In this way troglobitic populations originate by gradual adaptation to subterranean life; paedogenesis represents a coincident adaptation in this context. The local nature of this process ensures that cave populations originate independently, and at locally de-

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termined rates and times. The entire sequence of preadaptation to and colonization of caves (which are the drainage networks discharged by springs) thus proceeds in a parallel fashion, and fully satisfies the design criteria for a replicated natural experiment. Of the 26 known troglobitic populations of Eurycea, 13 clearly represent independent colonizations by populations of E. neotenes; another seven populations are very likely to be independently derived. The six remaining populations (of the advanced troglobite Eurycea tridentifera) appear to represent subterranean dispersal of a single ancestral population.

The selective regimes affecting troglobitic populations of Eurycea appear to be similar among cases as judged by the observed close correspondence in adaptations displayed by these populations. The suite of character state modifications found among troglobites displays a highly significant (nonrandom) pattern of concordance, which is within the range of concordance values observed in the ontogeny of single populations. Trophic adaptations are more concordant than are locomotor adaptations among troglobites; it is tempting (and probably valid) to conclude from this that evolutionary parallelism in trophic structures is more tightly constrained by selection than is parallel adaptation in locomotor structures. This interpretation is in accord with the generally accepted conclusion that feeding efficiency is of primary importance to animals in the cave environment. The other major modality in the evolution of troglobites is

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that of conservation of energy through increasingly efficient developmental and metabolic maintenance expenditure; *a prior*, this latter class of adaptations seems amenable to solution in more diverse ways than does the class of trophic adaptations in the Texas *Eurycea*.

The existence of parallelism on a broad scale and the largely allopatric distributions of troglobitic populations urges caution in the use of morphological similarity in the systematic evaluation of the diversity of troglobitic populations. Unless there is strong evidence of physical continuity among cave systems, morphological similarity must be interpreted as the result of similarity in the product of selection pressure and time divided by population size. Such assemblages represent grades rather than clades, and their taxonomic recognition is phylogenetically invalid insofar as nomenclature should reflect monophyly.

Major assistance in setting a base level for the degree of evolutionary divergence among populations of the Texas *Eurycea* is provided by three apparent cases of secondary contact involving *E. neotenes* and *E. tridentifera*. Actual sympatry between the two species is documented only at Honey Creek Cave; the interactions in the Cascade Caverns System and Valdina Farms Sinkhole are inferred from the characteristics of the resident populations. The opportunity for ecological isolation between epigean and troglobitic populations is present at Honey Creek Cave, and here *E. neotenes* and *E. tridentifera* interact as species. Only four of 70

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specimens from this site are hybrids. There is some evidence from a comparison of the other populations of E. neotenes of the middle Guadalupe valley that E. neotenes at Honey Creek Cave has been competitively excluded from the cave environment by E. tridentifera.

Opportunities for ecological isolation between populations of E. neotenes and E. tridentifera inferred to contact in the Cascade Caverns System and in Valdina Farms Sinkhole are lacking; in these sites the two populations appear to freely hybridize. The resultant populations show wide variability in character states, and in Valdina Farms Sinkhole the usual pattern of ontogenetic concordance in characters breaks down (as expected of a hybrid swarm).

These conclusions concerning the evolutionary development of the Texas Eurycea necessitate the systematic re-interpretation of described species. To date six species have been described and all have been generally accepted. These species are: Eurycea nana Bishop, 1941; Eurycea neotenes Bishop and Wright, 1937; Eurycea pterophila Burger, Smith and Potter, 1946; Eurycea latitans Smith and Potter, 1946; Eurycea troglodytes Baker, 1957; and Eurycea tridentifera Mitchell and Reddell, 1965. As a result of the present work the following nomenclatoral system is proposed (Table 18).

The small aquatic salamanders of the Edwards Plateau are correctly allocated to the genus Eurycea. Metamorphosed individuals of Eurycea neotenes are most similar to Eurycea

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Table 18. Summary of the taxonomic allocations of epigean and troglobitic populations of Texas *Eurycea*. Localities in parentheses denote parentage of hybrid populations.

SPECIES	LOCALITIES
Eurycea nana	San Marcos Springs
	Comal Springs
Eurycea neotenes	All other epigean sites
	Sutherland Hollow Cave
	Haby Water Cave
	T Cave
	Plumly Ranch Cave
	Bender's Cave
	Honey Creek Cave (part)
	Kneedeep Water Cave
	Little Water Cave
	Deadman's Cave
	Alzafar Water Cave
	Golden Fawn Cave
	Victor Phillip Water Cave
	Behr's Cave
	(Cascade Caverns System)
	(Valdina Farms Sinkhole)

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Eurycea neotenes concl.	Tucker Hollow Cave
	Salamander Cave
	Carson Cave
	Fourmile Cave
Eurycea sp.	Barton Springs
Eurycea tridentifera	Elm Springs Cave
	Honey Creek Cave (part)
	Kappelman Salamander Cave
	Calmbach Cave
	Grosser's Sinkhole
	Badweather Pit
	(Cascade Caverns System)
	(Valdina Farms Sinkhole)
Not allocated	Schwarz Cave
	Cave near Concan

multiplicata of the Interior Highlands, and paedogenetic individuals of E. neotenes are similar to the paedogenetic Eurycea tynerensis of the southwestern margin of the Ozark Plateau. No dichotomy of generic significance exists among the species here assigned to the genus Eurycea (contra Wake, 1966). The presently monotypic genus Typhlomolge is distinct from Eurycea and contains two species (Potter and Sweet, in preparation).

Eurycea nana has not been directly examined in this work, but unpublished data support its continued recognition. In addition to the type locality (San Marcos Springs, Hays County) E. nana also occurs in Comal Springs, Comal County.

The name Eurycea neotenes is herein applied to all other epigean populations, and to 17 troglobitic populations (Table 18) distributed across the Edwards Plateau from Travis County south and west to Val Verde County. Certain of these populations (notably Bender's Cave and Salamander Cave) may be incipient species, but in view of the apparent lack of genetic isolation characterizing the least- and most-advanced troglobitic taxa it is felt that their allocation to E. neotenes is evolutionarily realistic.

Eurycea pterophila Burger, Smith and Potter, 1950 is a junior synonym of Eurycea neotenes Bishop and Wright, 1937, by virtue of the fact that the described population is indistinguishable from E. neotenes.

Eurycea latitans Smith and Potter, 1946 of the Cascade Sinkhole System is placed in the synonymy of Eurycea neo-

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tenes (part) and Eurycea tridentifera Mitchell and Reddell, 1965 (part), for two reasons. First, the majority of its characteristics are well within the range of variation observed in other troglobitic populations of E. neotenes; and second, features separating E. latitans from E. neotenes result from limited hybridization with populations of E. tridentifera occurring in the same cave system on the Cibolo Sinkhole Plain.

Eurycea troglodytes Baker, 1957, is an invalid taxon which represents an unstable hybrid swarm involving individuals of E. neotenes and E. tridentifera. The name E. troglodytes is reduced to the synonymy of Eurycea neotenes (part) and Eurycea tridentifera (part). The holotypes of both E. latitans and E. troglodytes are hybrid individuals.

Eurycea tridentifera is a valid taxon, presently known from six cave localities in the southeastern corner of the Edwards Plateau (Table 18). Four of these populations occupy an interconnected cave system beneath the Cibolo Sinkhole Plain, which is also physically continuous with the caves of the Balcones Aquifer to the south. The occurrence of E. tridentifera at Honey Creek Cave in the middle Guadalupe valley is unusual in terms of the low probability of cave systems crossing major surface divides, but this population is not far removed from those of the Cibolo Sinkhole Plain. The Honey Creek Cave and Badweather Pit populations of E. tridentifera share a nondisjunct chromosome which passes meiosis (Bogart, 1967); other populations of E. tri-

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dentifera have not been examined, but this unique shared character is alone sufficient to argue against the occurrence of parallelism among these populations. The dubious criterion of morphological similarity provides no counter-argument to this interpretation.

The Barton Springs population (Travis County) represents an undescribed taxon of species rank. A name and diagnosis for this uniquely-specialized troglobitic population will be presented elsewhere.

With these modifications the current conception of the diversity of the Texas Eurycea is substantially changed. This viewpoint of an adaptive trend of troglobites extending from E. neotenes through E. latitans, E. troglodytes and E. tridentifera is simply invalid, as is the current argument that Typhlomolge rathbuni represents an end member of this continuum and is properly considered a species of Eurycea (Mitchell and Reddell, 1965; Mitchell and Smith, 1972). The apparent situation involves only two taxa having substantial ranges: Eurycea neotenes as a widespread epigean species which has repeatedly colonized cave environments under the influences of local environmental deterioration in an independent fashion; and Eurycea tridentifera, a widespread, advanced troglobitic species whose colonization of the cave environment apparently predates the ongoing process in populations of Eurycea neotenes. Eurycea nana and Eurycea sp. are specialized inhabitants of the Balcones Fault Zone, and do not contribute in significance to the major

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patterns of adaptive change which characterize the evolutionary development of the Texas Eurycea.

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Appendix I

This section provides locality and repository data for 95 epigean populations of Texas Eurycea (E. neotenes, 93; E. nana, 1; E. sp. nov.,1) whose origins have been precisely determined. Most of these populations were located during the course of field work; precise localities for other samples were acquired through communication with the collectors in cases where recorded data were insufficient. For other localities of collection for E. neotenes (some are doubtlessly duplications) see Appendix II.

Spring names are fully capitalized if the name appears on U.S.G.S. topographic maps, or is fixed in local usage; most localities are termed according to the nearest named drainage. Elevations are given in feet, and distances to the center of the nearest towns in miles to facilitate direct use of county and topographic maps in relocating populations. The coordinates of latitude and longitude for each site were taken from U.S.G.S. 7½' topographic maps, and will enable placement of each spring to within a zone of about 10 m in radius. These coordinates are the primary locality data; elevations are less useful, depending on the accuracy of mapping and the contour interval employed.

Abbreviations for collection numbers are as follows: A.M.N.H., American Museum of Natural History, New York; C.A.S., California Academy of Sciences, San Francisco; C.U., Cornell University, Ithaca; F.M.N.H., Field Museum of Natural

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History, Chicago; M.V.Z., Museum of Vertebrate Zoology, Berkeley; S.S.S., personal collection of the author, to be catalogued in the M.V.Z.; T.C.W.C., Texas Cooperative Wildlife Collection, College Station; and T.N.H.C., Texas Natural History Collection, Austin.

Bandera County

Pear Tree Spring, 1600': 29° 40' 44' N, 99° 11' 14" W; 7.5 mi. SW Bandera. M.V.Z. 119497-119499.

Indian Spring, 1600': 29° 40' 48" N, 99° 11' 14" W; 7.7 mi. SW Bandera. M.V.Z. 119500-119506.

Cazey Creek east spring, 1820': 29° 44' 15" N, 99° 20' 20" W; 7.3 mi. SW Medina. M.V.Z. 119350-119359.

Townsend Camp Hollow spring, 1810': 29° 44' 08" N, 99° 22' 07" W; 7.5 mi. SW Medina. M.V.Z. 119360-119377; 122833-122837.

Cazey Creek west spring, 1830': 29° 43' 44" N, 99° 22' 13" W; 8.4 mi. SW Medina. M.V.Z. 119378-119386.

Weed Bluff spring, 1910': 29° 44' 46" N, 99° 25' 25" W; 11.2 mi. SW Medina. M.V.Z. 119489-119496.

Sutherland Hollow spring, 1920-1940': 29° 44' 58" N, 99° 25; 40" W; 11.2 mi. SW Medina. M.V.Z. 119386-119488.

Devil's Bathtub Spring, 1940': 29° 47' 02" N, 99° 26' 33" W; 12.1 mi. WSW Medina. M.V.Z. 119629.

Clement Springs, 1620': 29° 42' 49" N, 99° 17' 22" W; 4.7 mi. NW Tarpley. M.V.Z. 119507-119601.

Hondo Creek tributary spring, 1600': 29° 42' 24" N, 99°

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21' 30" W; 7.0 mi. NW Tarpley. M.V.Z. 119602.

Hondo Creek spring, 1675': 29° 43' 09" N, 99° 22' 12" W; 7.4 mi. NW Tarpley. M.V.Z. 119603-119610.

Seco Creek spring, 1700': 29° 42' 42" N, 99° 24' 58' W; 9.9 mi. NW Tarpley. M.V.Z. 119611-119628.

Mill Creek spring, 1940': 29° 47' 30" N, 99° 30' 10' W; 4.6 mi. NE Vanderpool. T.N.H.C. 21673 (41 specimens); M.V.Z. 119630-119743.

Wedgeworth Creek north spring, 1850': 29° 48' 33" N, 99° 33' 55" W; 4.6 mi. N Vanderpool. M.V.Z. 119804-119935; 122828-122840.

Wedgeworth Creek south spring, 1820': 29° 47' 48" N, 99° 33' 53" W; 4.2 mi. N. Vanderpool. M.V.Z. 119760-119803.

Sabinal River headwaters spring, 1840': 29° 49' 34" N, 99° 34' 00" W; 5.4 mi. N Vanderpool. T.N.H.C. 21676 (five specimens); T.T.U. uncatalogued (13 specimens).

Bell County

Salado Springs (eastern outlet on Lazy Days Fish Farm), 570': 30° 56' 36" N, 97° 32' 09" W; 0.4 mi. NE Salado. Private collection of B.C. Brown, Baylor University.

Bexar County

Clear Fork Cibolo Creek spring, 960': 29° 41' 44" N, 99° 23' 48" W; 5.3 mi. SE Bulverde (Comal Co.). M.V.Z. 11954-120026; 122802-122812.

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Bexar County concl.

Cherry Spring and Walnut Spring, 940', 950': 29° 40' 58" N, 99° 24' 00" W, 29° 40' 48" N, 99° 23' 59" W; 6.3, 6.6 mi. SE Bulverde (Comal Co.). C.U. 4194 (seven specimens); 4427 (12 specimens); 4450 (16 specimens); C.A.S. 7596; 80984

Leon Springs, 1160': 29° 39' 46" N, 98° 38' 12" W; 0.6 mi. W Leon Springs. M.V.Z. 120095-120101.

Helotes Creek spring, 1240': 29° 38' 15" N, 98° 41' 40" W; 4.2 mi. N Helotes. T.N.H.C. T6295-T6302; 21671 (4 specimens); U.S.N.M. 103161 (type of E. neotenes); F.M.N.H. 36845; 91036-91038; 91039 (13 specimens); 91053; T.T.U. uncatalogued (5 specimens); M.V.Z. 120027-120094.

Culebra Creek spring, 1130': 29° 35' 05" N, 98° 45' 40" W; 4.0 mi. WSW Helotes. M.V.Z. 120102-120104.

Blanco County

Boardhouse Spring, 1300': 30° 06' 40" N, 98° 18' 07" W; 7.2 mi. ENE Blanco. M.V.Z. 120105-120154.

Cove Branch Creek spring, 1240': 30° 03' 58" N, 98° 20' 47" W; 4.5 mi. ESE Blanco. M.V.Z. 120156.

Blanco River spring, 1300': 30° 05' 45" N, 98° 25' 10" W; Blanco. M.V.Z. 120157-120166.

Zercher Spring, 1340': 30° 06' 10" N, 98° 27' 25" W; 1.9 mi. W Blanco. T.C.W.C. uncatalogued.

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Comal County

Comal Springs, 630': 29° 42' 45" N, 98° 08' 14" W; and 29° 42' 48" N, 98° 08' 12" W; New Braunfels. T.N.H.C. 6234 (8 specimens); M.V.Z. 120392-120465.

Bear Creek spring, 1020': 29° 48' 12" N, 98° 15' 17" W; 4.7 mi. ESE Smithson Valley. S.S.S. 13617-13622.

Dry Bear Creek spring, 1060': 29° 48' 57" N, 98° 14' 48" W; 5.2 mi. WSW Sattler. M.V.Z. 120270-120273.

Bailey Ranch spring, 950': 29° 53' 48" N, 98° 08' 12" W; 4.8 mi. NE Sattler. M.V.Z. 120255-120269.

Devil's Backbone spring, 1120': 29° 55' 50" N, 98° 09' 33" W; 5.4 mi. N Sattler. A.M.N.H. 60790; M.V.Z. 120167-120254.

Rebecca Creek Spring, 1080': 29° 55' 57" N, 98° 22' 22" W; 3.9 mi. NE Spring Branch. T.C.W.C. 44515-44522; 44534; M.V.Z. 120274-120276.

Puter (Turkey) Creek spring, 1140': 29° 55' 57" N, 98° 23' 20" W; 3.5 mi. NE Spring Branch. M.V.Z. 120277-120381.

Honey Creek Cave spring, 1100': 29° 50' 51" N, 98° 29' 30" W; 5.8 mi. SW Spring Branch. M.V.Z. 120382-120383; 120385-120388.

Edwards County

Dutch Creek spring, 1860': 29° 39' 10" N, 100° 06' 12" W; 6.8 mi. SW Barksdale. M.V.Z. 120598-120731; 122815-122820.

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Edwards County concl.

Pulliam Creek spring, 1800': 29° 50' 04" N, 100° 07' 25" W; 9.2 mi. NW Barksdale. M.V.Z. 120732-120776.

Spring Creek spring, 1640': 29° 41' 28" N, 100° 07' 42" W; 6.1 mi. WSW Barksdale. M.V.Z. 120777.

Trough Springs, 1900': 30° 08' 36" N, 99° 04' 13" W; 8.0 mi. N. Kerrville (Kerr Co.). M.V.Z. 120778-120822.

Cottonwood Spring, 2010': 30° 10' 32" N, 99° 09' 58" W; 7.8 mi. N Kerrville (Kerr Co.). T.N.H.C. T6303-T6314.

House Spring, 1900': 30° 08' 11" N, 99° 14' 18" W; 4.8 mi. N Ingram (Kerr Co.). M.V.Z. 120874-120883; T.C.W.C. 44504-44508; CS-113 - CS-119; CS-127 - CS-130.

Hays County

San Marcos Spring, 580': 29° 53' 38" N, 97° 55' 47" W; San Marcos. (E. nana) T.C.W.C. 1501-1516; 4168-4191; 4366-4370; 13252-13274; 14393-14394; 14492-14493; 15052-15054; 17398; 17488-17496; 18518-18519; 21087-21089; 23134-23149; 26809-26820; 30742-30752; 34917-34921; 3182-3185; 30509; CS-135 - CS-148; C.U. 4433 (12 specimens); M.V.Z. 120964-121194; 122821. Note - partial listing; moast major collections have series of E. nana.

Fern Bank (Little Arkansas) Spring, 800': 29° 59' 00" N,

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Hays County concl.

98° 00' 45" W; 5.2 mi. E Wimberley. (E. pterophila) T.C.W.C. 13104; 13701-13709; 14182-14183; 17575-17577; 18520-18526; 26825-25830; 33293-33294; 34922-34929; CS-120 - CS-124; CS-131 - CS-134; S-203 - S-204; M.V.Z. 120884-120938. Note - partial listing; most major collections have series from this population.

Cypress Creek spring, 850': 29° 59' 55" N, 98° 06' 03" W; 0.3 mi. NNW Wimberley. M.V.Z. 120939-120963.

Kendall County

East Curry Creek spring, 1240': 29° 57' 45" N, 98° 32' 18" W; 1.1 mi. WSW Kendalia. T.C.W.C. 44523-44529; M.V.Z. 121195-121205.

Victor Phillip Water Cave spring, 1260': 29° 52' 57" N, 98° 40' 51" W; 6.9 mi. NNE Boerne. M.V.Z. 121206-121227.

Brown's Creek spring, 1400': 29° 47' 45" N, 98° 44' 27" W; 1.8 mi. E Boerne. T.C.W.C. 44509-44514.

Balcones Creek spring, 1470': 29° 44' 18" N, 98° 44' 27" W; 3.2 mi. SSW Boerne. M.V.Z. 121228.

Cibolo Creek tributary spring, 1810': 29° 48' 30" N, 98° 51' 44" W; 8.2 mi. WNW Boerne. M.V.Z. 121229-121339.

Bear Creek spring, 1800': 29° 48' 15" N, 98° 52' 10" W; 8.3 mi. WNW Boerne. M.V.Z. 121340-121367.

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Kerr County

Ayala Spring, 1830': 30° 03' 26" N, 99° 04' 25" W; 4.0 mi. ENE Kerrville. M.V.Z. 121396-121403.

Quinlan Creek tributary spring, 1810': 30° 05' 11" N, 99° 05' 28" W; 4.3 mi. NE Kerrville. M.V.Z. 121404.

176 Spring, 1870': 30° 05' 18" N, 99° 19' 14" W; 1.6 mi. NNE Hunt. T.C.W.C. CS-108 - CS-112; M.V.Z. 121405-121466.

Unnamed creek spring, 1860': 30° 01' 00" N, 99° 21' 06" W; 4.0 mi. S Hunt. M.V.Z. 121524-121543.

Fessenden Branch spring, 1890': 30° 09' 58" N, 99° 21' 03" W; 1.7 mi. SE Mountain Home. M.V.Z. 121467-121484.

Honey Creek spring, 1900': 30° 06' 02" N, 99° 21' 42" W; 2.8 mi. NW Hunt. M.V.Z. 121485-121586.

North Fork Guadalupe River spring, 1880': 30° 03' 04" N, 99° 26' 54" W; 7.1 mi. WSW Hunt. M.V.Z. 121487.

Lange Ravine east spring, 1860': 30° 01' 57" N, 99° 23' 05" W; 3.9 mi. SW Hunt. M.V.Z. 121488-121522.

Lange Ravine west spring, 1860': 30° 01' 57" N, 99° 23' 07" W; 4.0 mi. SW Hunt. M.V.Z. 121423.

Edmunson Creek east spring, 1900': 30° 00' 23" N, 99° 21' 44" W; 5.8 mi. SSW Hunt. M.V.Z. 121544-121558.

Edmunson Creek west spring, 1880': 30° 00' 21" N, 99° 21' 54" W; 5.8 mi. SSW Hunt. M.V.Z. 121559-121561.

Buffalo Creek spring, 1900': 29° 58' 18" N, 99° 22' 35" W; 6.5 mi. SW Hunt. M.V.Z. 121562-121583.

Chimney Spring, 1884': 30° 00' 19" N, 99° 24' 25" W; 6.2

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Kerr Co. concl.

mi. SW Hunt. M.V.Z. 121584-121594.

Cherry Creek spring, 1910': 30° 00' 34" N, 99° 24' 38" W; 6.3 mi. SW Hunt. M.V.Z. 121595-121617.

Fall Creek spring, 1910': 29° 54' 45" N, 97° 12' 20" W; 9.6 mi. SSW Kerrville. M.V.Z. 121670-121894.

Lambs Creek spring, 1900': 29° 55' 20" N, 99° 14' 21" W; 10.6 mi. SW Kerrville. M.V.Z. 121895-122831.

Turtle Creek spring, 1980': 29° 59' 06" N, 99° 15' 51" W; 8.0 mi. SW Kerrville. M.V.Z. 121617-121669.

Robinson Creek spring, 1840': 29° 54' 55" N, 99° 15' 08" W; 8.1 mi. NNW Medina (Bandera Co.). M.V.Z. 122078-122090.

Wallace Creek spring, 1700': 29° 54' 48" N, 99° 17' 52" W; 8.7 mi. NNW Medina (Bandera Co.). M.V.Z. 122091-122093.

Medina County

Seco Creek spring, 1310': 29° 35' 17" N, 99° 23' 58" W; 2.8 mi. SSE jct. Bandera, Medina and Uvalde cos. M.V.Z. 122125-122129.

Richter Springs, 1400': 29° 35' 32" N, 99° 23' 07" W; 9.4 mi. SE Utopia (Uvalde Co.). M.V.Z. 122094.

New Pump Spring, 1580': 29° 36' 14" N, 99° 21' 42" W; 10.4 mi. ESE Utopia (Uvalde Co.). M.V.Z. 122095-122108.

Yellow Spring, 1525': 29° 36' 56" N, 99° 22' 05" W; 10.7

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Medina County concl.

mi. E Utopia (Uvalde Co.). M.V.Z. 122109-122124.

Real County

West Sabinal River tributary spring, 1620': 29° 41' 13" N, 99° 37' 22" W; 7.6 mi. NW Utopia (Uvalde Co.). T.N.H.C. 21669 (17 specimens); 21670.

Harris Spring, 1640': 29° 43' 24" N, 99° 37' 10" W; 9.2 mi. NW Utopia (Uvalde Co.). T.N.H.C. 21674 (40 specimens).

Ash Hollow spring, 1840': 29° 44' 07" N, 99° 38' 37" W; 8.4 mi. ENE Leadey. M.V.Z. 122142-122364.

Mud Spring, 1910': 29° 40' 30" N, 99° 40' 02" W; 5.0 mi. NE Rio Frio. M.V.Z. 122377-122398.

Little Dry Frio Creek tributary spring, 1800': 29° 43' 12" N, 99° 40' 10" W; 7.0 mi. E Leakey. M.V.Z. 122365-122376.

South Prong Cypress Creek north spring, 1830': 29° 47' 58" N, 99° 38' 54" W; 9.3 mi. NE Leakey. M.V.Z. 122399-122407.

South Prong Cypress Creek south spring, 1910': 29° 47' 46" N, 99° 39' 58" W; 9.2 mi. NE Leakey. T.C.W.C. CS-149 - CS-150; M.V.Z. 122408-122476; 122832.

East Frio River spring, 1850': 29° 51' 02" N, 99° 40' 02" W; 11.6 mi. NE Leakey. M.V.Z. 122477-122587.

Bee Cave Hollow spring, 2030': 29° 54' 25" N, 99° 47' 27" W; 11.0 mi. N Leakey. M.V.Z. 122592-122671.

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Real County concl.

Short Prong Frio River spring, 2000': 29° 55' 00" N, 99° 47' 30" W; 12.0 mi. N Leakey. M.V.Z. 122588-122591.

Prade Ranch spring, 1950': 29° 54' 51" N, 99° 47' 02" W; 12.0 mi. N Leakey. F.M.N.H. 55086 (2 specimens); 55087-55090; 55092-55093; 55095-55096.

Old Faithful Spring, 1460': 29° 40' 48" N, 100° 00' 51" W; 0.5 mi. N Camp Wood. M.V.Z. 122672.

Mullen Hollow spring, 1940': 29° 57' 57" N, 99° 57' 52" W; 9.0 mi. NNE Barksdale (Edwards Co.). M.V.Z. 122673-122686.

Travis County

Barton Springs, 440': 30° 15' 51" N, 97° 46' 10" W; 1.9 mi. SW State Capitol, Austin. (*Eurycea* sp. nov.) T.N.H.X. T6317-T6321; T.T.U. uncatalogued (22 specimens); M.V.Z. 122712-122736; S.S.S. 13623-13633.

Stillhouse Hollow spring, 780': 30° 22' 20" N, 97° 45' 45" W; 6.9 mi. NNW State Capitol, Austin. M.V.Z. 122695-122703.

McDonald Well spring, 770': 30° 26' 57" N, 97° 51' 12" W; 3.1 mi. NNW Four Points (Hickmuntown). T.C.W.C. 44530-44532; CS-125 - CS-126; M.V.Z. 122705-122711.

Uvalde County

Onion Creek spring, 1500': 29° 34' 57" N, 99° 34' 51" W; 3.9 mi. SW Utopia. M.V.Z. 122764-122767.

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Uvalde County concl.

Salt Marsh Creek spring, 1800': 29° 37' 03" N, 99° 36' 06" W; 4.2 mi. W Utopia. M.V.Z. 122727-122763.

Bludworth Ranch spring, 1500': 29° 31' 40" N, 99° 39' 12" W; 10.6 mi. SW Utopia. M.V.Z. 122768-122774.

Montell Creek spring, 1530': 29° 43' 28" N, 100° 04' 48" W; 5.2 mi. NW Montell. M.V.Z. 122775.

Val Verde County

San Felipe Springs, 910': 29° 22' 22" N, 100° 53' 09" W; 0.9 mi. ENE Del Rio. M.V.Z. 122791-122792.

Williamson County

San Gabriel River spring, 660': 30° 39' 15" N, 97° 40' 01" Wl 1.3 mi. NNE Georgetown. M.V.Z. 122801.

Krienke Spring, 800': 30° 30' 22" N, 97° 44' 54" W; 3.2 mi. NW Round Rock. T.N.H.C. T1802-T1816; T6334-T6339; 31013 (42 specimens).

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Appendix II

This section provides existing data for a maximum of 46 populations of Eurycea neotenes which were not possible to locate to the degree necessary for inclusion in Appendix I. A number of these appear to represent erroneous notations, and a certain number may be from sites listed in Appendix I.

Localities preceded by an asterisk are included on Figure 8. Abbreviations of collections are listed in Appendix I, save for T.A.&I.C., Texas A&I University Collection, Kingsville.

Bandera County

18 mi. NW Medina, Sutton Ranch. T.N.H.C. T2182-T2183.

23 mi. N Medina (probably 23 mi. NW Medina, as listed by Baker, 1961). T.N.H.C. T1886 (4 specimens).

7 mi. E Vanderpool, tributary of Mill Creek. T.N.H.C. 20807 (6 specimens).

Populations are reported from Bandera Creek, 6 mi. N Medina, and Middle Verde Creek, 8 mi. SW Bandera, by B.C. Brown, Baylor University (pers. com., 1970).

Bell County

No additional localities.

Bexar County

Helotes Creek, 5 mi. N Helotes. T.N.H.C. T6295-T6302; T.C.W.C. CS-151; K.U. 22229.

Culebra Creek, Helotes. F.M.N.H. 108596-108601.

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Bexar County concl.

Helotes, creek on Melton's. T.N.H.C. 21671 (4 specimens).

Blanco County

1/4 and 3/4 mi. SE Blanco (Baker, 1961).

Waggoner's Cove spring, 4.0 mi. SE Blanco (F.S. Hendricks, pers. com., 1971).

Comal County

Voges Springs, Vogus (sic) Ranch, at KLRN radio transmitter. (pers. com., A. Hamilton, 1973).

Fishers Store, spring to NE. (pers. com., B.C. Brown, 1971).

Spring on Bear Creek, 4 mi. SW Sattler. T.T.U. uncatalogued (1 specimen).

Edwards County

4 mi. NW of Pulliam Creek, Barksdale. T.N.H.C. 20799 (19 specimens).

Gillespie County

*Fredericksburg. T.C.W.C. 14160-14163.

N Fredericksburg, Wolf Creek. T.C.W.C. 14118. (Note - Wolf Creek extends SW from Fredericksburg, and joins the Pedernales River SE of Fredericksburg; thus the indication "N" is probably in error).

Hays County

San Marcos Springs - this locality appears in a number of

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Hays County concl.

ways, some of them erroneous. Aquarena Springs and Brown School are strict synonyms. Presumably inaccurate notations include: 1 mi. W San Marcos (T.C.W.C. 1512, 1514); 5 mi. E San Marcos (T.C.W.C. 4369); and San Marcos (numerous specimens).

Fern Bank Spring - this locality is widely reported as being 6.3 mi. NE Wimberley, following an error in the type description. Other presumably erroneous notations for this frequently visited site include: 6 mi. N Wimberley (T.C.W.C. 13275); 4 mi. SE Wimberley (T.C.W.C. 13701-13709; 14182, 14183); 4 mi. E Wimberley (T.C.W.C. 26827-26830); 3-4 mi. E Wimberley (T.C.W.C. 17575-17577).

1 mi. SE Fern Bank Springs. T.C.W.C. 26821-26824.

Wilson Creek, near Wimberley (A. Hamilton, pers. com., 1973).

Wimberley, along Blanco River 100 yards W highway 32 bridge (A. Hamilton, pers. com., 1973).

Spring near Twin Sister Mountain, 2 mi. from Wimberley (Uhlenhuth, 1921).

12 mi. WNW San Marcos on Skyline Ranch, Wimberley. T.N.H.C. 19290.

Rio Bonito Camp spring, on Blanco River (A. Hamilton, pers. com., 1973).

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Kendall County

5 mi. N Boerne (Baker, 1961).

5 mi. WNW Boerne, W.M. Thornton Ranch (Baker, 1961).

*5.5 mi. WNW Boerne. T.N.H.C. 4824.

8 mi. W Boerne, Hall Ranch (Baker, 1961).

Several localities on Joshua Creek, near Welfare (B.C. Brown, pers. com., 1970).

Kerr County

6 mi. NNW Kerrville. T.N.H.C. T2314-T2316.

5 mi. W Kerrville, Turtle Creek (Baker, 1961). (Locality probably in error, as Turtle Creek is 7-12 mi. SW of Kerrville.)

8.3 mi. S, 2½ mi. W Kerrville, M.L. Pampell Ranch, tributary of Turtle Creek T.N.H.C. 11931 (Milstead, 1951).

13 mi. SW Kerrville, Chaney Ranch, 29° 54' 30" N, 99° 12' 30" W. T.A.&I.C. 1064 (63 specimens); 1308 (22 specimens); 1669 (117 specimens); 1822 (19 specimens); 2209 (27 specimens); 2480 (2 specimens); 3179 (108 specimens). Note - these collections combine specimens from Lambs Creek, Fall Creek, and the drainage of Verde Creek (A.H. Chaney, pers. com., 1973).

15 mi. SW Kerrville. K.U. 60769-60771.

Medina County

No additional localities reported.

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Real County

10 mi. NE Leakey, Cypress Creek, spring. T.N.H.C. 21677 (36 specimens).

10 mi. NE Leakey, spring on East Frio River. T.N.H.C. 21675 (44 specimens).

15 mi. N Leakey, Moffit Ranch. T.C.W.C. 24452-24454.

15 mi. from Leakey. T.C.W.C. 23886.

Spring of Hours, Prade Ranch. F.M.N.H. 55097-55107; 55009; 55111-55122.

Travis County

*Spring near Marshall Ford Dam (Mansfield Dam) (Baker, 1961).

*Jack Dies Ranch, near Dodd City. T.N.H.C. 21640-21643.

Uvalde County

*Spring on bank of Frio River, about 2 mi. S of Garner State Park. T.C.W.C. 2114-2119; CS-166.

*Montell Springs, Montell. T.N.H.C. 21658-21659.

Montell Creek. T.N.H.C. 21672.

Val Verde County

No additional localities reported.

Williamson County

*1½ mi. NE Round Rock, Brushy Creek. T.N.H.C. 6242.

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Appendix III

This section provides locality data for 55 springs visited during the course of field work which were apparently not inhabited by *Eurycea neotenes*. The format is the same as in Appendix I.

Bandera County

Kindla Spring, 1260': 29° 44' 54" N, 99° 06' 54" W.

Elm Creek spring, 1680': 29° 46' 06" N, 99° 17' 18" W.

North Prong Medina River spring, 1650': 29° 51' 25" N, 99° 21' 45" W.

Bell County

Salado Springs, 560': 30° 56' 23" N, 97° 32' 06" W.

Bexar County

San Antonio Springs, 680': 29° 27' 56" N, 98° 28' 06" W.

Blanco County

290x281 spring, 1280': 30° 12' 32" N, 98° 22' 28" W.

Crabapple Creek spring, 1380': 30° 06' 08" N, 98° 30' 35" W.

Comal County

Frio Spring, 1100': 29° 55' 55" N, 98° 10' 46" W.

Lonesome Valley Spring, 1060': 29° 56' 00" N, 98° 10' 21" W.

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Kendall County

Simmons Creek spring, 1080': 29° 54' 53" N, 98° 29' 57" W.

Little Water Cave creek spring, 1100': 29° 53' 16" N, 98° 31' 10" W.

Alzafar creek spring, 1280': 29° 53' 00" N, 98° 39' 19" W.

Swede Creek spring, 1180': 29° 52' 02" N, 98° 34' 38" W.

Panther Creek spring, 1100': 29° 52' 18" N, 98° 32' 42" W.

Fourlevel Water Cave spring, 1808': 29° 52' 41" N, 98° 31' 33" W.

Kerr County

Hasenwinkle Creek spring, 1800': 30° 04' 14" N, 98° 57' 40" W.

Cross Creek Ranch spring, 1850': 30° 06' 57" N, 98° 57' 40" W.

East Town Creek spring, 1820': 30° 05' 58" N, 99° 07' 31" W.

Lange Box Spring, 2000': 30° 02' 05" N, 99° 23' 45" W.

Guadalupe headwaters spring, 1920': 30° 03' 10" N, 99° 29' 42" W.

Bee Caves Creek lower spring, 1900': 30° 03' 30" N, 99° 27' 33" W.

Bee Caves Creek upper spring, 1940': 30° 02' 13" N, 99° 25' 21" W.

Johnson Creek spring, 1900': 30° 10' 46" N, 99° 22' 45" W.

Honey Creek Ranch spring, 1900': 30° 06' 12" N, 99° 22' 07" W.

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Edwards County

Pulliam Creek lower spring, 1800': 29° 50' 22" N, 100° 07' 19" W.

Pulliam Creek upper spring, 1820': 29° 51' 02" N, 100° 07' 45" W.

Gillespie County

Spring Creek spring, 2010': 30° 20' 35" N, 99° 04' 48" W.

Live Oak Creek spring, 2020': 30° 21' 08" N, 99° 01' 26" W.

Pecan Creek spring, 2000': 30° 22' 03" N, 98° 58' 22" W.

Willow Creek spring, 1900': 30° 21' 51" N, 98° 45' 48" W.

Hays County

Smith Creek lower spring, 1080': 30° 01' 02" N, 98° 04' 27" W.

Smith Creek upper spring, 1100': 30° 01' 35" N, 98° 04' 45" W.

Ben McCulloch Spring, 940': 30° 07' 40" N, 98° 00' 45" W.

Blanco River spring, 820': 29° 59' 32" N, 98° 05' 30" W.

spring 1.5 mi E Payton, 1270': 30° 06' 33" N, 98° 16' 08" W.

Rancho Cima Dam spring, 1040': 29° 56' 23" N, 98° 09' 06" W.

spring 1 mi SE Signal Hill, 880': 30° 10' 48" N, 97° 56' 07" W.

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Kinney County

Las Moras Springs, 1100': 29° 18' 32" N, 100° 25' 16" W.

Real County

Deer Creek spring, 1620': 29° 39' 27" N, 99° 40' 03" W.

Eagle Cliff spring, 1880': 29° 57' 38" N, 99° 57' 12" W.

Travis County

Sheep Hollow spring, 980': 30° 35' 08" N, 97° 58' 07" W.

Spicewood Springs, 730': 30° 21' 55" N, 97° 44' 59" W.

Canyon Spring, 1020': 30° 15' 35" N, 97° 53' 03" W.

Short Spring Branch spring, 850': 30° 15' 00" N, 97° 53' 18" W.

Uvalde County

Bear Creek lower spring, 1700': 29° 36' 18" N, 99° 36' 50" W.

Bear Creek upper spring, 1740': 29° 36' 39" N, 99° 36' 30" W.

Cowan Springs, 1260': 29° 30' 17" N, 99° 42' 27" W.

Cold Springs Ranch Spring, 1410': 29° 36' 45" N, 99° 44' 25" W.

Concan Springs, 1220': 29° 29' 47" N, 99° 42' 40" W.

Williamson County

Andice spring, 970': 30° 46' 58" N, 97° 50' 16" W.

Sycamore Springs, 990': 30° 48' 48" N, 97° 55' 33" W.

S Fork San Gabriel spring, 850': 30° 37' 06" N, 97° 50' 40" W.

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Williamson County concl.

Jim Hagg Road spring, 830': 30° 40' 31" N, 97° 45' 38" W.

Crockett Gardens Springs, 810': 30° 39' 50" N, 97° 45' 05" W.

Sideriver spring, 760': 30° 36' 00" N, 97° 45' 00" W.

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Appendix IV

This section provides locality data for the 29 known or reported troglobitic populations of the Texas *Eurycea*, and lists specimen numbers and repositories of the available material. The form of citation employed in Appendix I is retained here, with the modification that locality data refer to the cave entrance rather than the point(s) in the cave inhabited by salamanders. Additional abbreviations: D.B.W., David B. Wake, Museum of Vertebrate Zoology; and U.S.N.M., United States National Museum of Natural History.

Bandera County

Sutherland Hollow Cave, 1800': 29° 45' 02" N, 99° 25' 18" W; 10.9 mi. SW Medina. No specimens.

Haby Water Cave, 2270': 29° 51' 45" N, 99° 33' 38" W; 7.8 mi. NNE Vanderpool. M.V.Z. 119936; T.T.U. uncatalogued (1 specimen).

Bexar County

Elm Springs Cave, 965': 29° 35' 00" N, 98° 34' 00" W; 0.8 mi SSE junction of highways 1604 and 1535, San Antonio. S.S.S. 13640-13643; T.C.W.C. 38237; 44494; CS-159; CS-160.

Blanco County

T Cave, 1180': 30° 04' 36" N, 98° 19' 46" W; 0.75 mi SSW junction of Boardhouse Creek and Blanco River, 6.0 mi. E Blanco. No specimens.

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Comal County

Fischer's Well, 1140': 29° 58' 53" N, 98° 15' 36" W; in settlement of Fischer. T.T.V. uncatalogued (1 specimen).

Plumly Ranch Cave, 1100': 29° 54' 23" N, 98° 26' 39" W; 3.1 mi. NW Spring Branch. No specimens.

Bender's Cave, 1100': 29° 53' 55" N, 98° 26' 42" W; 2.8 mi. NW Spring Branch. M.V.Z. 120466-120530; 122814; T.T.U. uncatalogued (5 specimens).

Honey Creek Cave, 1100': 29° 50' 51" N, 98° 29' 30" W; 5.8 mi. SW Spring Branch. E neotenes: M.V.Z. 120382-120383; 120385-120388; intermediate morph: M.V.Z. 120384; 120389-120391; E. tridentifera: M.V.Z. 120531-120560; T.N.H.C. 31521-31534 (paratypes); T.C.W.C. 44484-44486; CS-162; T.T.U. uncatalogued (10 specimens); U.S.N.M. 153780 (holotype); 153781-153785 (paratypes); D.B.W. 421-423.

Kappelman Salamander Cave, 1035': 29° 45' 46" N, 98° 23' 08" W; 3.0 mi. SE junction highways 46 and 281, 16 mi. WNW New Braunfels. S.S.S. 13505-13507; T.T.U. uncatalogued (2 specimens).

Calmbach Cave, 1180': 2.2 02.4 mi. NW Bulverde. T.T.U. uncatalogued (1 specimen).

Grosser's Sinkhole, 1270': 29° 44' 52" N, 98° 36' 48" W; 6.0 mi. SSW Bergheim. M.V.Z. 120583-120597; T.T.U. uncatalogued (4 specimens) T.C.W.C. 44487-44488; CS-158.

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Comal County concl.

Badweather Pit, 1280': 29° 45' 21" N, 98° 37' 13" W; 5.5 mi. SW Bergheim. M.V.Z. 120561-120582; T.T.U. uncatalogued (20 specimens); T.C.W.C. 44489-44492; CS-161.

Kendall County

Kneedeep Water Cave, 1100': 5.2-6.5 mi. W Spring Branch, N bank Guadalupe River. No specimens.

Little Water Cave, 1100': 29° 53' 18" N, 98° 31' 11" W; 5.4 mi. NE Bergheim. No specimens.

Deadman's Cave, 1140': 29° 53' 10" N, 98° 37' 01" W; 10.0 mi. NE Boerne. M.V.Z. 121377-121391.

Alzafar Water Cave, 1260': 29° 53' 05" N, 98° 39' 19" W; 8.3 mi. NE Boerne. M.V.Z. 121368-121375; T.C.W.C. 44502-44503; 45354; CS-155 - CS-157.

Golden Fawn Cave, 1260': 29° 53' 00" N, 98° 40' 10" W; 7.4 mi. NNE Boerne. M.V.Z. 121376.

Victor Phillip Water Cave, 1260': 29° 52' 57" N, 98° 40' 51" W; 6.9 mi. NNE Boerne. M.V.Z. 121206-121227.

Behr's Cave, 1340': 29° 55' 51" N, 98° 42' 20" W; 10.3 mi. N Boerne. M.V.Z. 121392-121395.

Cascade Caverns, 1320': 29° 45' 48" N, 98° 40' 42" W; 3.3 mi. SE Boerne. U.S.N.M. 123594 (holotype); T.C.W.C. 1195-1197; T.N.H.C. 4822, 6326, 6331-6333; C.U. 4551; F.M.N.H. 91040, 91041, 91043, 91054; M.V.Z. 68381, 68382; T.T.U. uncatalogued (2 specimens).

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Kendall County concl.

Cascade Sinkhole, 1320': 29° 45' 49" N, 98° 40' 53" W; 3.2 mi. SE Boerne. S.S.S. 13634-13639; T.T.U. uncatalogued (2 specimens).

Schwarz Cave, 1340': 29° 44' 40" N, 98° 40' 37" W; 4.5 mi. SE Boerne. No specimens.

Medina County

Valdina Farms Sinkhole, 1210': 29° 30' 58" N, 99° 23' 58" W; 15.2 mi. NNW D'Hanis. T.N.H.C. 21791 (holotype); 21786-21790, 21792-21805 (paratypes); M.V.Z. 122130-122141; D.B.W. 424, 828; T.T.U. uncatalogued (7 specimens); T.C.W.C. 38233, 38235, CS-168.

Real County

Tucker Hollow Cave, 1880': 29° 44' 33" N, 99° 46' 42" W; 1.6 mi. NW Leakey. M.V.Z. 122687-122694; T.T.U. uncatalogued (2 specimens).

Travis County

Barton Springs, 440': 30° 15' 51" N, 97° 46' 10" W; 1.9 mi. SW Capitol, Austin. T.N.H.C. 6317-6321; M.V.Z. 122712-122726; S.S.S. 13623-13633, 15006-15031; T.T.U. uncatalogued (22 specimens).

Salamander Cave, 800': 30° 22' 03" N, 97° 45' 14" W; 6.5 mi. NNW Capitol, Austin. T.T.U. uncatalogued (8 specimens).

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Uvalde County

Cave near Concan: probably Bludworth Ranch, 4-6 mi. NE Concan. No specimens.

Carson Cave, 1480': 29° 28' 50" N, 100° 04' 44" W. 5.1 mi. SW Montell. M.V.Z. 122776-122790.

Val Verde County

Fourmile Cave, 1070': 29° 25' 33" N, 100° 53' 23" W; 3.6 mi. N Del Ril. T.N.H.C. 21678 (4 specimens, now missing); M.V.Z. 122793-122800; T.T.U. uncatalogued (1 specimen).

Comstock Crack, 1400': 29° 41' 25" N, 101° 11' 28" W; 1.0 mi. WNW Comstock. No specimens.

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Appendix V

Localities and respositories of cleared and stained specimens of Eurycea pterophila, E. nana, and E. neotenes examined in Chapter VII. General localities are followed by coordinates of latitude and longitude. Abbreviations: M.V.Z.: Museum of Vertebrate Zoology, University of California, Berkeley; T.C.W.C.: Texas Cooperative Wildlife Collection, Texas A and M University; T.N.H.C.: Texas Natural History Collection, University of Texas, Austin; T.T.U.: uncatalogued material, Dr. R. W. Mitchell, Texas Tech University.

Eurycea pterophila (33 specimens), Hays County, Fern Bank Spring (29° 59' 00" N, 98° 00' 45" W): M.V.Z. 120923-120938; M.V.Z.-DBW 231-233. T.C.W.C. CS-120 - CS-124; CS-131 - CS-134. T.N.H.C. 31004 (five specimens).

Eurycea nana (40 specimens),Hays County, San Marcos Spring (29° 53' 38" N, 97° 55' 47" W): M.V.Z. 121042-121067. T.C.W.C. CS-135 - CS-148.

Eurycea neotenes (59 specimens), Bandera County, Mill Creek (29° 47' 30" N, 99° 30' 10" W): M.V.Z. 119937-119952. Bexar County, 5 miles (=8 km) N Helotes (29° 38' 15" N, 98° 41' 40" W): M.V.Z. 120027-120034, 120069. T.C.W.C. CS-151. Comal County, Bender's Cave (29° 53' 55" N, 98° 26' 42" W): M.V.Z. 120487-120492. Gillespie County, Henderson Branch (30° 08' 11" N, 99° 14' 18" W): T.C.W.C. CS-113 - CS-119, CS-127 - CS-130. Kendall

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County, Alzafar Water Cave (29° 53' 05" N, 98° 39' 19" W): T.C.W.C. CS-155 - CS-157. Kerr County, Fessenden Branch (30° 09' 58" N, 99° 21' 03" W): M.V.Z. 121480-121483; Lambs Creek (29° 55' 20" N, 99° 14' 21" W): M.V.Z. 121929-121931. Real County, Cypress Creek (29° 47' 46" N, 99° 38' 58" W): T.C.W.C. CS-149, CS-150; East Frio River (29° 47' 46" N, 99° 40' 02" W): M.V.Z. 122541; 15 miles (=24 km) N Leakey: T.C.W.C. CS-167. Travis County, Salamander Cave (30° 22' 03" N, 97° 45' 14" W): T.T.U. SC-1 - SC-3.

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