

The Evolutionary Development of the Texas Eurycea

(Amphibia: Plethodontidae)

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by

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Part 2

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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-

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).

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

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 geomorphology of the Edwards Plateau

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 the 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

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

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

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

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 ground-water 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

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,

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.

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.

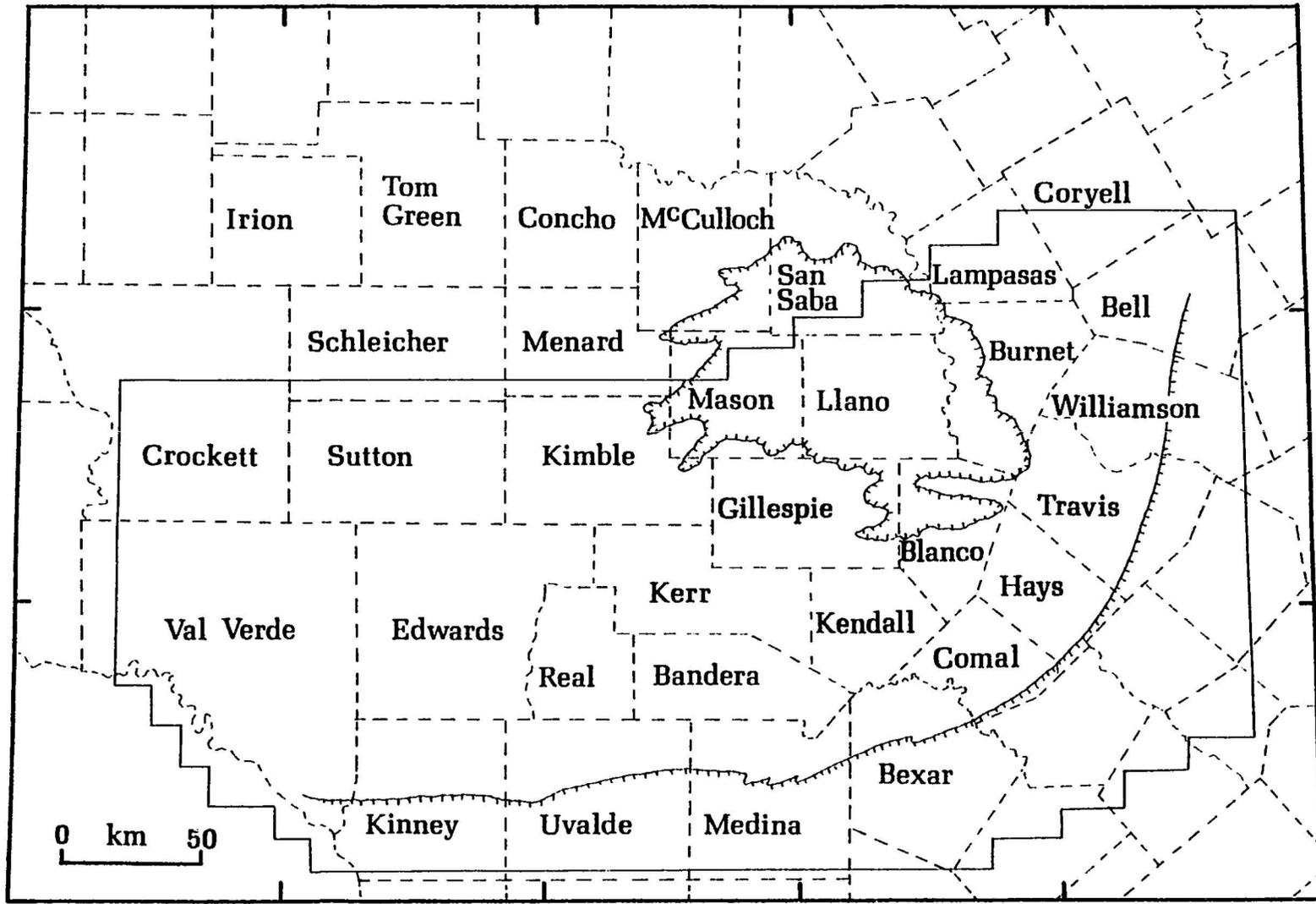
The present chapter details the distribution of epigean (surface dwelling) populations of Eurycea neotenes, and seeks to identify the determinants of this distribution in the geologic structure and hydrologic characteristics of the Plateau. The analysis is composed of several parts. Following a general 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.

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 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

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).



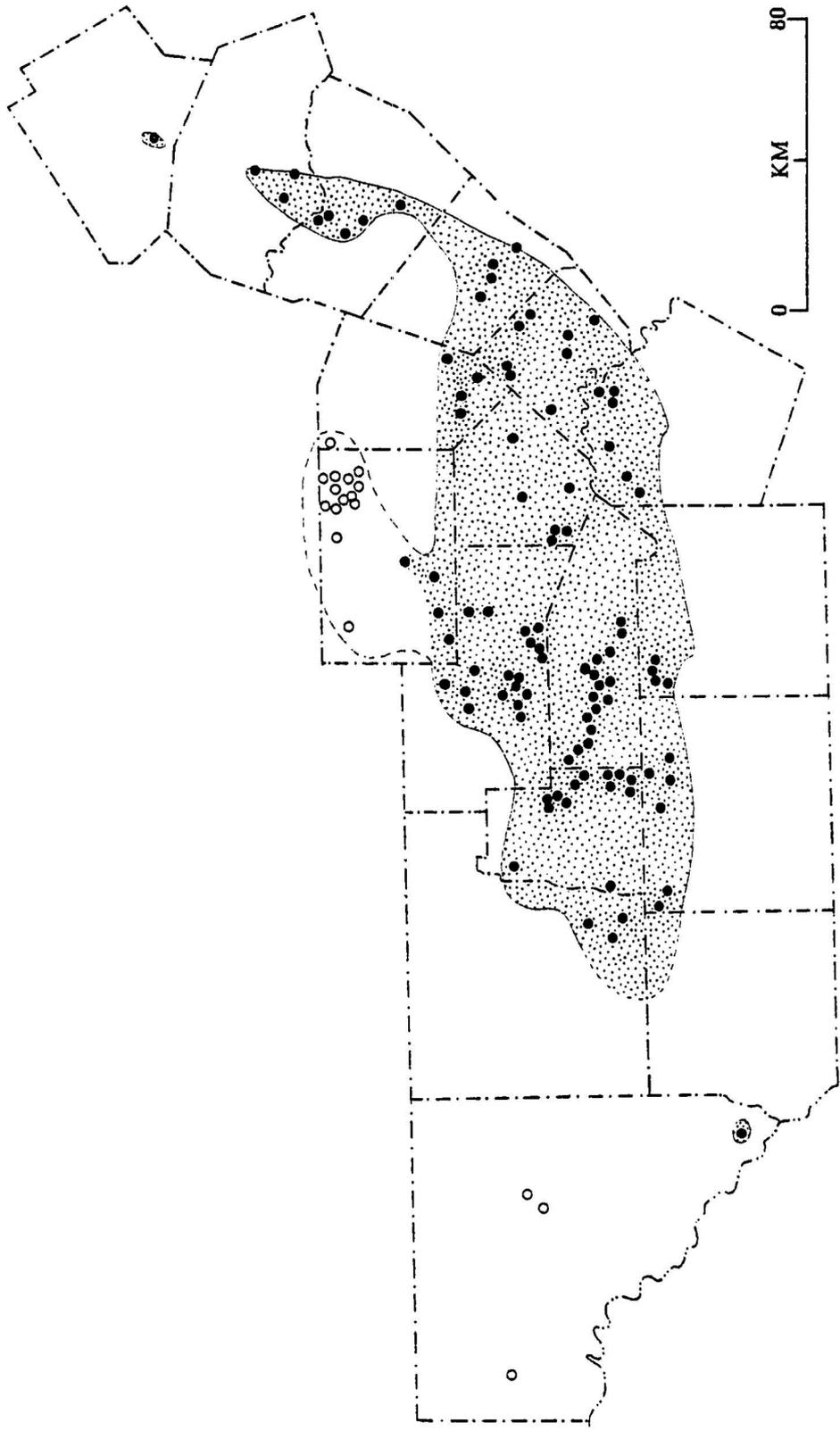
this survey are available from the author. This region encompasses the Balcones Fault Zone and the adjacent Gulf Coastal Plain as well as the major part of the Edwards Plateau and Llano Uplift. The known distribution of the Texas Eurycea comprises about 127 7½' quadrangles roughly centered within this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

Results and Discussion

Distribution of Epigeal 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 epigeal 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.

Figure 8. Distribution of epigeal 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.



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

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 epigeal 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

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 epigeal 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

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

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 epigeal 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 epigeal populations of Eurycea

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.

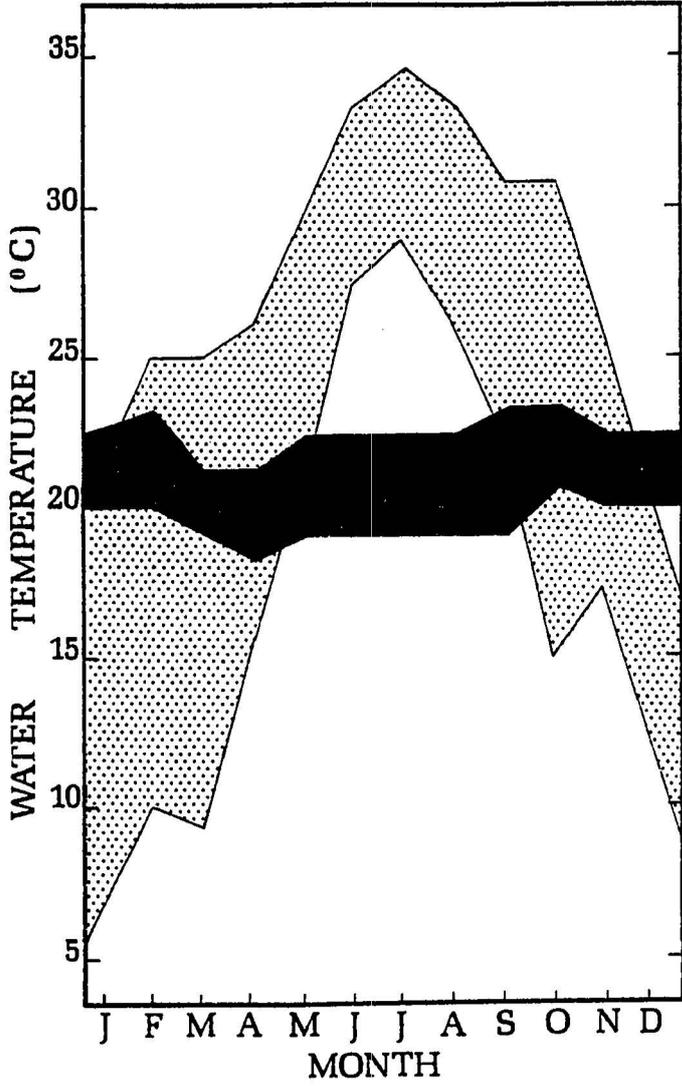
Several general correlates of the known distribution of epigeal populations of the Texas Eurycea can be drawn from the information at hand, including: (1) the restriction of populations to regions of limestone outcrop; (2) the virtual restriction of populations to the immediate vicinity of springs; (3) 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 epigeal 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 epigeal populations of Eurycea neotenes are restricted to the vicinity of springs, at least during the summer months (comparable data are not

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,

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.



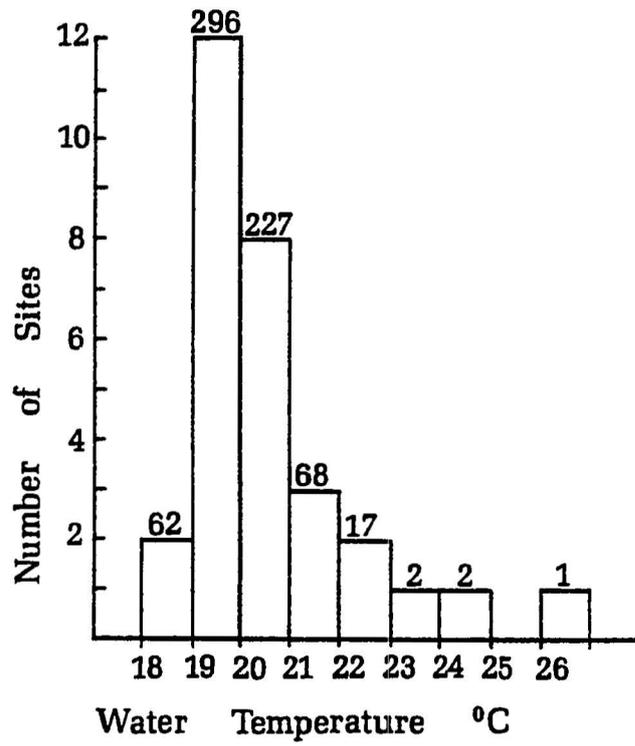
the deep circulating water discharged by the artesian springs of the Balcones Fault Zone is typically 1-2° C warmer than that of adjacent water-table springs.

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

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.



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 impermeous 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

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

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 analysis 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).

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 Edwards 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

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

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 continuously 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-

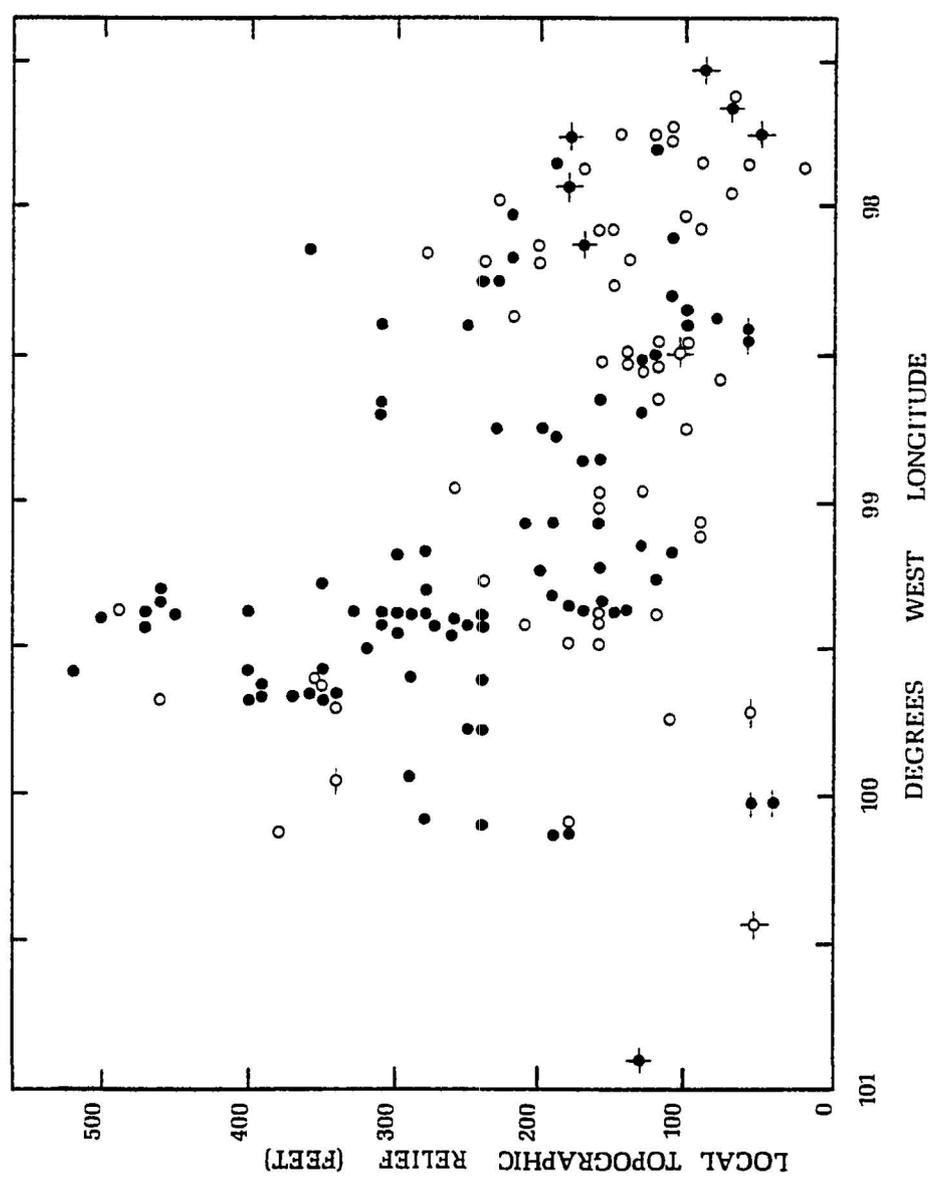
faces of isolated hills and narrow divides, whereas the springs at the headwaters of major drainages are supplied through a broad expanse of undissected Plateau surface.

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

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 $99^{\circ} 30' W$ 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

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).

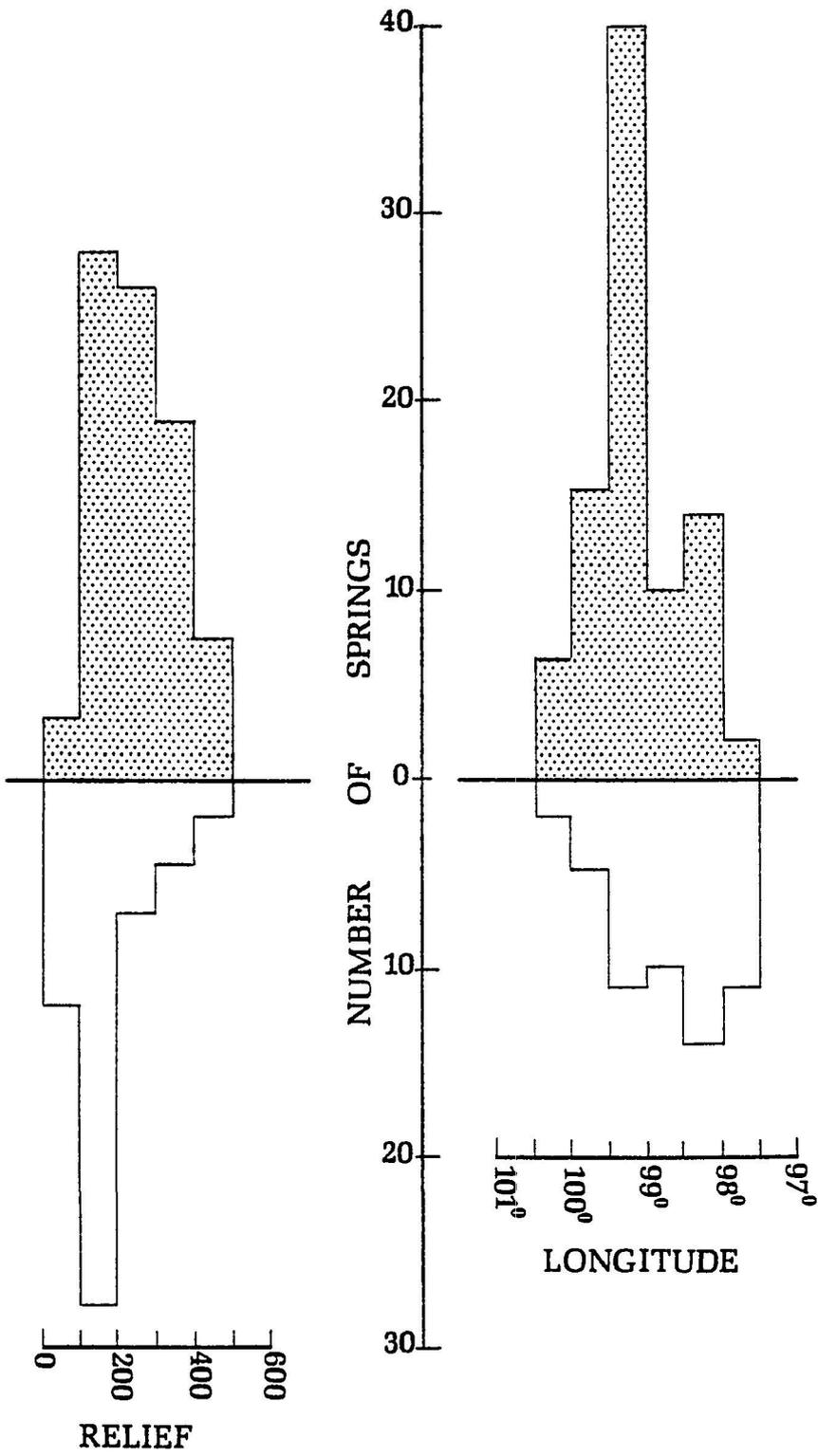


springs to appear in the eastern region of low local topographic relief, and demonstrates the concentration of populations of E. neotenes in the west central portion of the overall range.

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, $\chi^2=23.4$; $p < 0.001$), 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, $\chi^2=24.9$; $p < 0.001$). Fault zone springs were excluded from this anal-

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.



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:

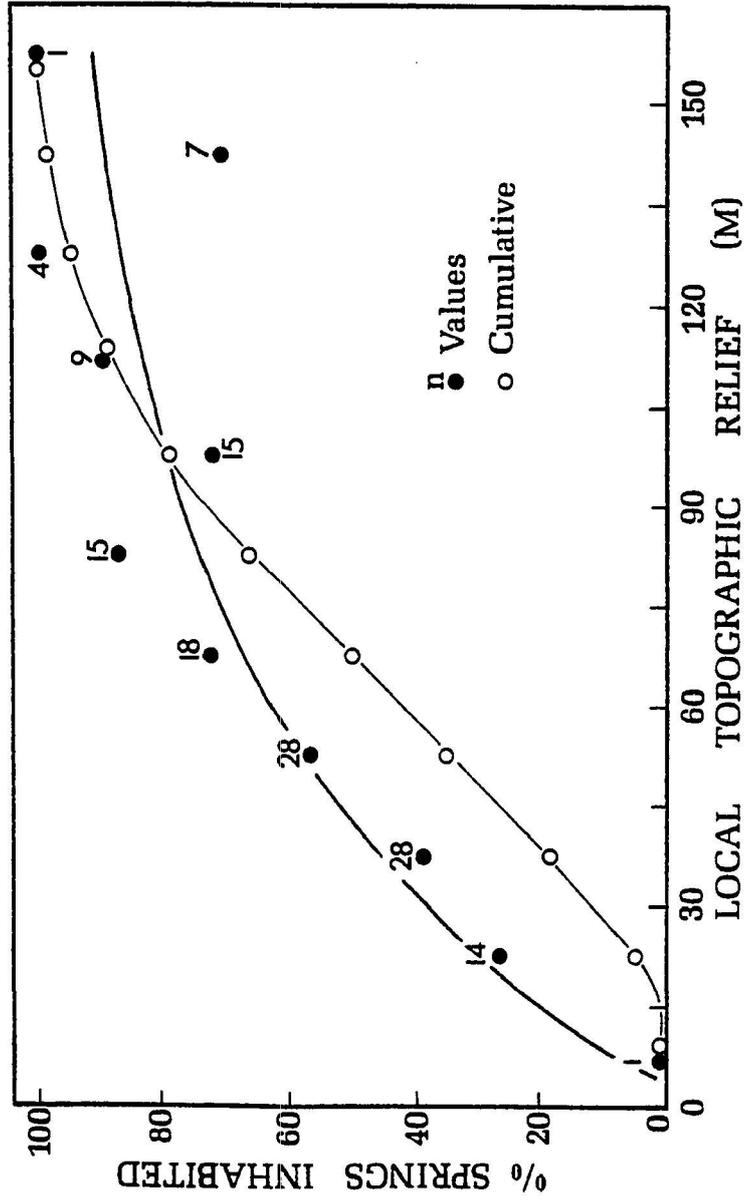
$$P = 0.634(\log R) - 0.531 \quad (r = 0.93)$$

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-

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

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



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

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.

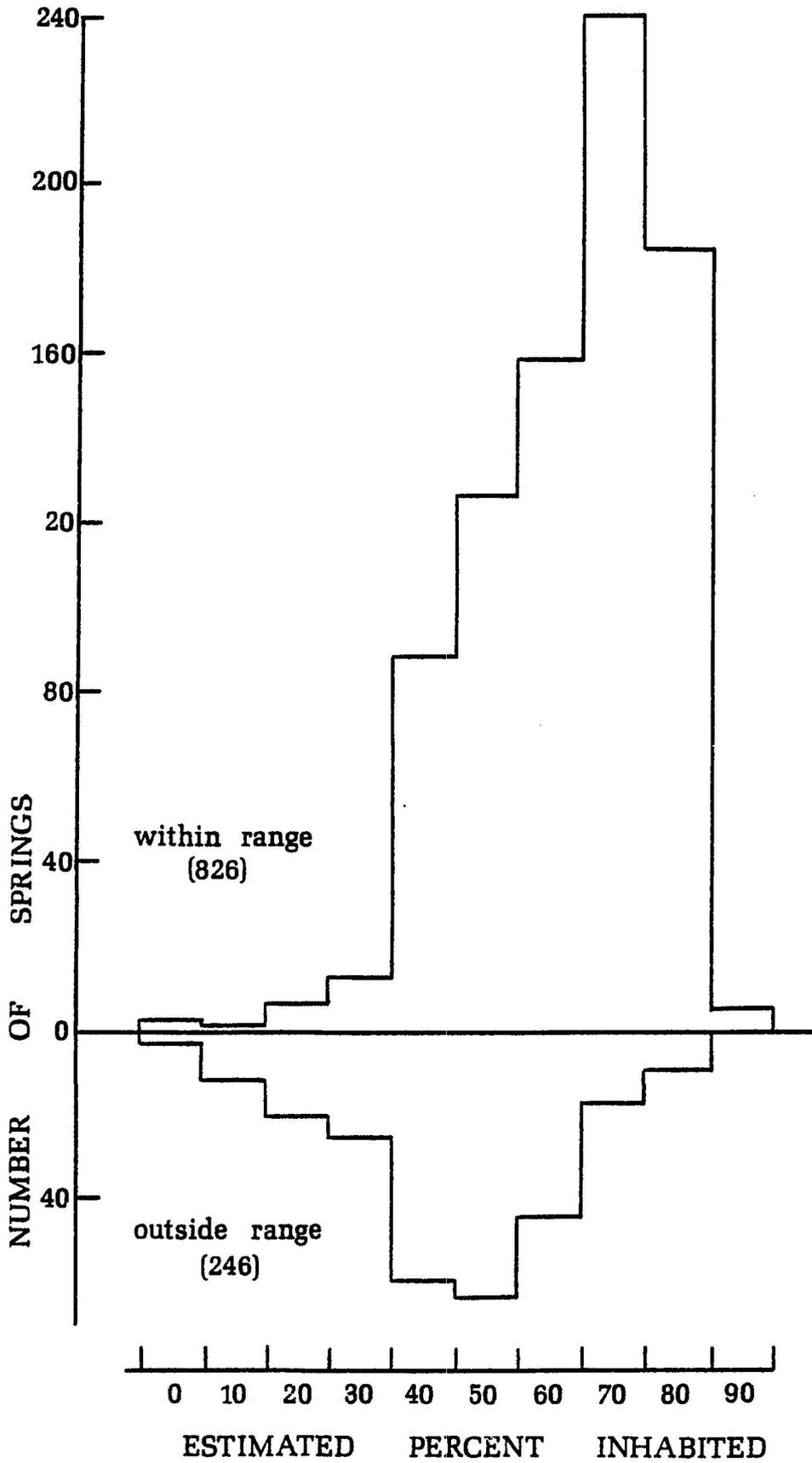


Table 3. Numbers of marked springs on 468 7½' topographic maps enclosing the known distribution of the Texas Eurycea. The areal extent of the region surveyed is shown in Figure 7. Underlined entries indicate quadrangles wholly or partially within the known range of Eurycea neotenes (see Figure 8).

	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	<u>0</u>	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	<u>2</u>	<u>12</u>	<u>0</u>	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	<u>10</u>	<u>8</u>	<u>0</u>	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	<u>0</u>	<u>1</u>	<u>0</u>	0	0	0		
I	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	-	-	-	-	9	7	<u>12</u>	<u>16</u>	<u>0</u>	0	0	0	0	1	<u>2</u>	<u>0</u>	<u>0</u>	0	0	0		
J	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	<u>2</u>	<u>3</u>	<u>1</u>	<u>3</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>6</u>	<u>6</u>	<u>2</u>	<u>2</u>	<u>1</u>	<u>0</u>	0	0	0	0		
K	1	0	0	0	0	3	0	0	0	0	0	0	<u>8</u>	0	0	0	<u>1</u>	<u>21</u>	<u>13</u>	<u>4</u>	<u>23</u>	<u>26</u>	<u>10</u>	<u>6</u>	<u>2</u>	<u>0</u>	<u>8</u>	<u>5</u>	<u>5</u>	<u>0</u>	<u>0</u>	0	0	0	0		
L	0	0	0	0	0	1	0	0	0	<u>2</u>	<u>1</u>	<u>1</u>	<u>7</u>	<u>31</u>	<u>13</u>	<u>7</u>	<u>0</u>	<u>9</u>	<u>14</u>	<u>8</u>	<u>0</u>	<u>3</u>	<u>0</u>	<u>2</u>	<u>2</u>	<u>3</u>	<u>2</u>	<u>0</u>	<u>0</u>	<u>0</u>	0	0	0	0	0		
M	0	0	0	0	0	0	0	0	0	<u>1</u>	<u>0</u>	<u>1</u>	<u>34</u>	<u>43</u>	<u>12</u>	<u>4</u>	<u>4</u>	<u>25</u>	<u>12</u>	<u>5</u>	<u>1</u>	<u>12</u>	<u>3</u>	<u>3</u>	<u>6</u>	<u>2</u>	<u>1</u>	<u>2</u>	<u>0</u>	0	0	0	0	0	0		
N		0	1	0	0	0	0	0	0	<u>2</u>	<u>1</u>	<u>10</u>	<u>33</u>	<u>9</u>	<u>43</u>	<u>8</u>	<u>14</u>	<u>37</u>	<u>14</u>	<u>10</u>	<u>8</u>	<u>15</u>	<u>11</u>	<u>0</u>	<u>11</u>	<u>0</u>	<u>0</u>	0	0	0	0	0	0	0	0		
O			0	0	0	0	0	0	0	0	<u>5</u>	<u>12</u>	<u>15</u>	<u>9</u>	<u>2</u>	<u>14</u>	<u>3</u>	<u>15</u>	<u>3</u>	<u>9</u>	<u>0</u>	<u>8</u>	<u>3</u>	<u>0</u>	<u>0</u>	0	0	0	0	0	0	1	0				
P				0	1	1	<u>1</u>	0	2	0	0	<u>1</u>	<u>0</u>	<u>4</u>	<u>0</u>	<u>0</u>	<u>1</u>	0	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	0	2							
R							0	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).

	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	<u>34</u>	<u>53</u>	<u>0</u>	0	0	0	11		
G	0	0	0	0	0	0	0	0	0	0	0	51	53	0	0	0	29	0	59	53	51	58	64	62	0	34	67	67	<u>61</u>	<u>48</u>	<u>0</u>	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	<u>0</u>	<u>37</u>	<u>0</u>	0	0	0	0		
I	0	0	0	0	0	0	0	0	0	0	0	0	0	64	-	-	-	-	-	53	53	<u>46</u>	<u>48</u>	<u>0</u>	0	0	0	0	18	<u>41</u>	<u>0</u>	<u>0</u>	0	0	0	0		
J	0	0	0	0	0	0	0	0	0	0	0	0	68	57	0	0	0	<u>51</u>	<u>54</u>	<u>46</u>	<u>54</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>58</u>	<u>56</u>	<u>47</u>	<u>53</u>	<u>59</u>	<u>0</u>	0	0	0	0	0		
K	81	0	0	0	0	71	0	0	0	0	0	0	<u>73</u>	0	0	0	<u>59</u>	<u>61</u>	<u>58</u>	<u>61</u>	<u>64</u>	<u>53</u>	<u>48</u>	<u>56</u>	<u>53</u>	<u>0</u>	<u>46</u>	<u>53</u>	<u>48</u>	<u>0</u>	<u>0</u>	0	0	0	0	0		
L	0	0	0	0	0	84	0	0	0	<u>58</u>	<u>65</u>	<u>84</u>	<u>82</u>	<u>72</u>	<u>70</u>	<u>65</u>	<u>0</u>	<u>62</u>	<u>62</u>	<u>63</u>	<u>0</u>	<u>66</u>	<u>0</u>	<u>61</u>	<u>53</u>	<u>53</u>	<u>48</u>	<u>0</u>	<u>0</u>	<u>0</u>	0	0	0	0	0	0		
M	0	0	0	0	0	0	0	0	0	<u>72</u>	<u>0</u>	<u>81</u>	<u>78</u>	<u>75</u>	<u>83</u>	<u>72</u>	<u>72</u>	<u>66</u>	<u>81</u>	<u>78</u>	<u>48</u>	<u>56</u>	<u>58</u>	<u>61</u>	<u>53</u>	<u>53</u>	<u>65</u>	<u>65</u>	<u>0</u>	0	0	0	0	0	0	0		
N		0	48	0	0	0	0	0	0	0	<u>73</u>	<u>62</u>	<u>68</u>	<u>83</u>	<u>79</u>	<u>81</u>	<u>82</u>	<u>80</u>	<u>77</u>	<u>74</u>	<u>56</u>	<u>67</u>	<u>72</u>	<u>70</u>	<u>0</u>	<u>68</u>	<u>0</u>	<u>0</u>	0	0	0	0	0	0	0	0		
O			0	0	0	0	0	0	0	0	<u>70</u>	<u>62</u>	<u>78</u>	<u>75</u>	<u>61</u>	<u>73</u>	<u>86</u>	<u>86</u>	<u>77</u>	<u>72</u>	<u>0</u>	<u>67</u>	<u>64</u>	<u>0</u>	<u>0</u>	0	0	0	0	0	0	0	0	29	0			
P				0	29	29	<u>29</u>	0	34	0	0	<u>65</u>	<u>0</u>	<u>84</u>	<u>0</u>	<u>0</u>	<u>73</u>	0	0	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	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	0	0	0	0	0	0	0	0	0	0	0

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

be estimated by inspection of the two $7\frac{1}{2}$ ' 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 epigeal 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

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 continuously 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 $\geq 70\%$ 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

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

The 26 peripheral springs of $\geq 70\%$ 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 $\geq 70\%$ 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 $\geq 70\%$ probability of habitation are

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-

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 $\geq 70\%$ 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 temporarily 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

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

Epigeal 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

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 neo-tenes 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 epigeal 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

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

grades of shared troglobitic adaptations within the set of populations; and fourth, to offer systematic interpretations from the viewpoint of the present analyses 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 epigeal 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

Figure 15. The distribution of troglobitic populations of Eurycea on the Edwards Plateau. Counties are outlined, and the solid line marks the range of epigeal 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.



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 an 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-

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 epigeal populations, the majority of trogloditic 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

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

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

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).

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-

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

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

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

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

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

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.

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.

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 iridophores. A

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

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

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

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-

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.

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-

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

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-

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-

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

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

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 Boggart (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

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

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-

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 occurrence 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-

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

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; Vandell, 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-

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 (<u>E. neotenes</u>)					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 (<u>E. tridentifera</u>)	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			

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,

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

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.