The Evolutionary Development of the Texas *Eurycea*

(Amphibia: Plethodontidae)

exclusive of pages 270-311 and 387-407

by

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# Part 4

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

### Discriminant Analysis

Discriminant analysis seeks to maximize the differences present in a character matrix representing two or more specified groups, producing character weightings which define the location of individuals in discriminant space through one or more linear functions. The discriminating power of the technique can easily exceed the validity of its interpretation; discrimination of samples per se must be interpreted with special caution. The approach here is to use the results in a relative, comparative fashion in an effort to discern both unusual levels of within-group variation and instances of failure in the classification of specimens to their pre-assigned groups. The relative positions of specified groups in discriminant space are also of interest in analyses which encompass the range of an adaptive trend such as the series of troglobitic populations considered here.

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

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

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

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

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

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

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

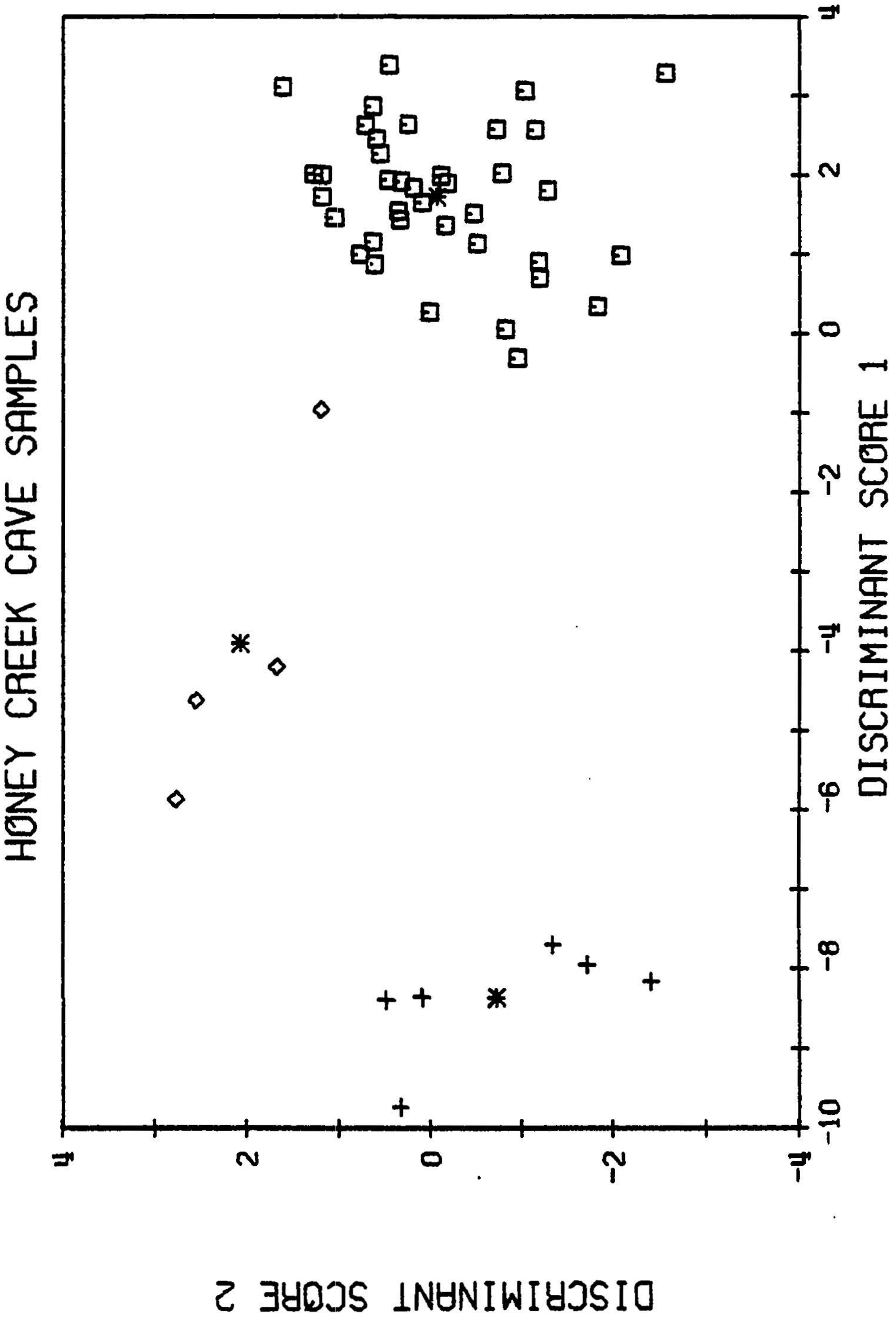

HONEY CREEK CAVE SAMPLES
DISCRIMINANT SCORE 1
DISCRIMINANT SCORE 2
-10
-8
-6
-4
-2
0
2
4
-4
-2
0
2
4

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

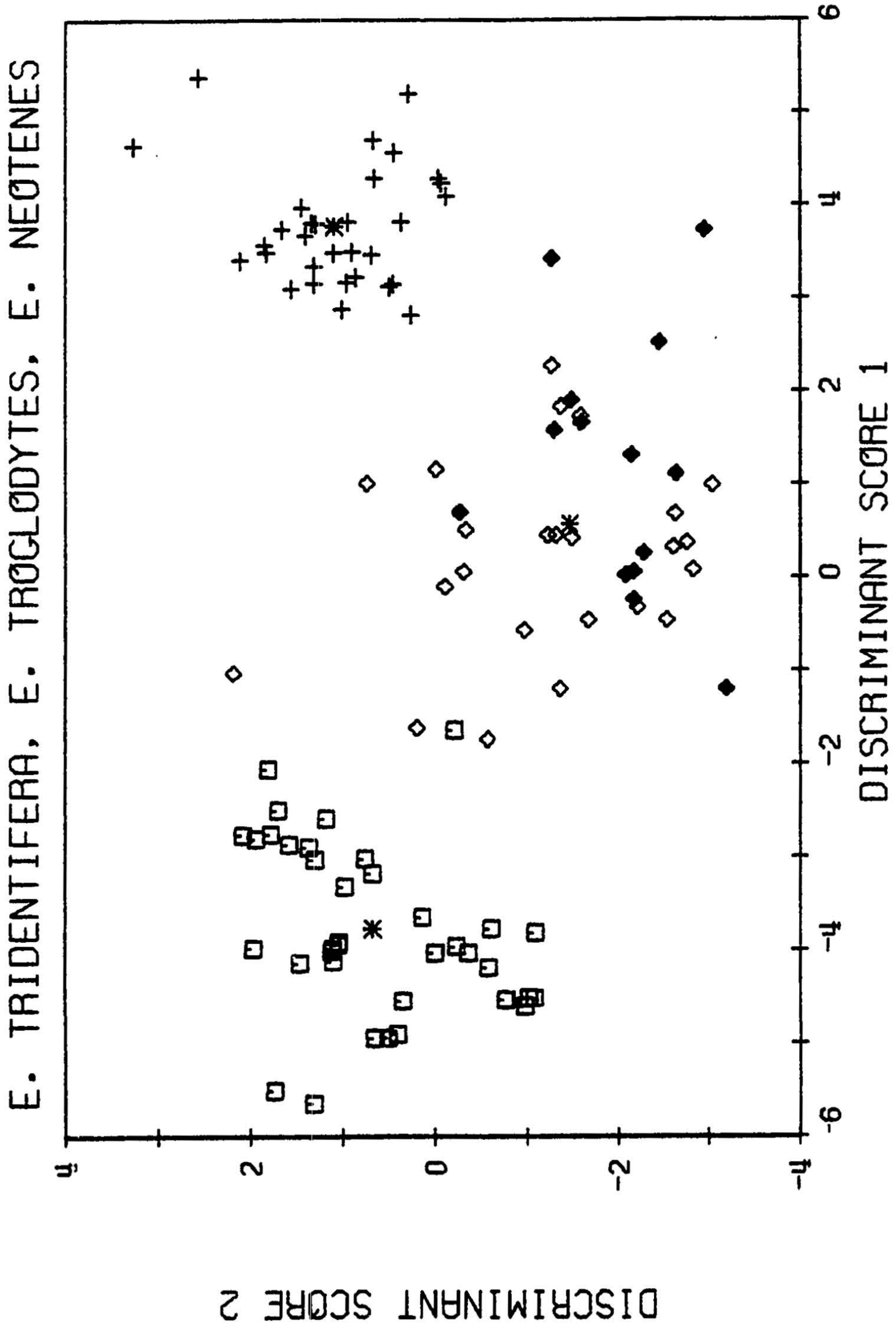

E. TRIDENTIFERA, E. TROGLODYTES, E. NEOTENES
DISCRIMINANT SCORE 1
DISCRIMINANT SCORE 2
-6
-4
-2
0
2
4
6
4
2
0
-2
-4

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

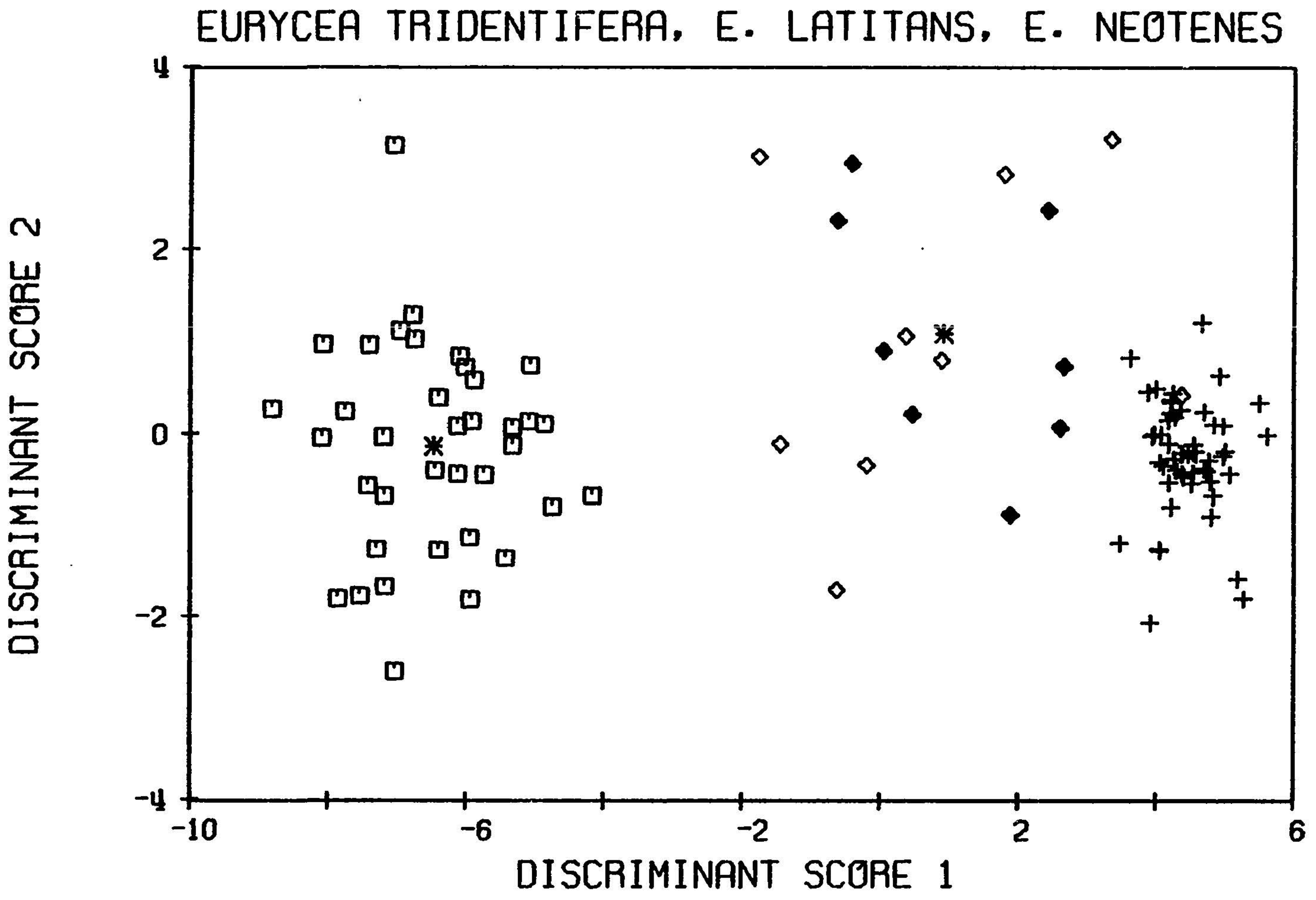
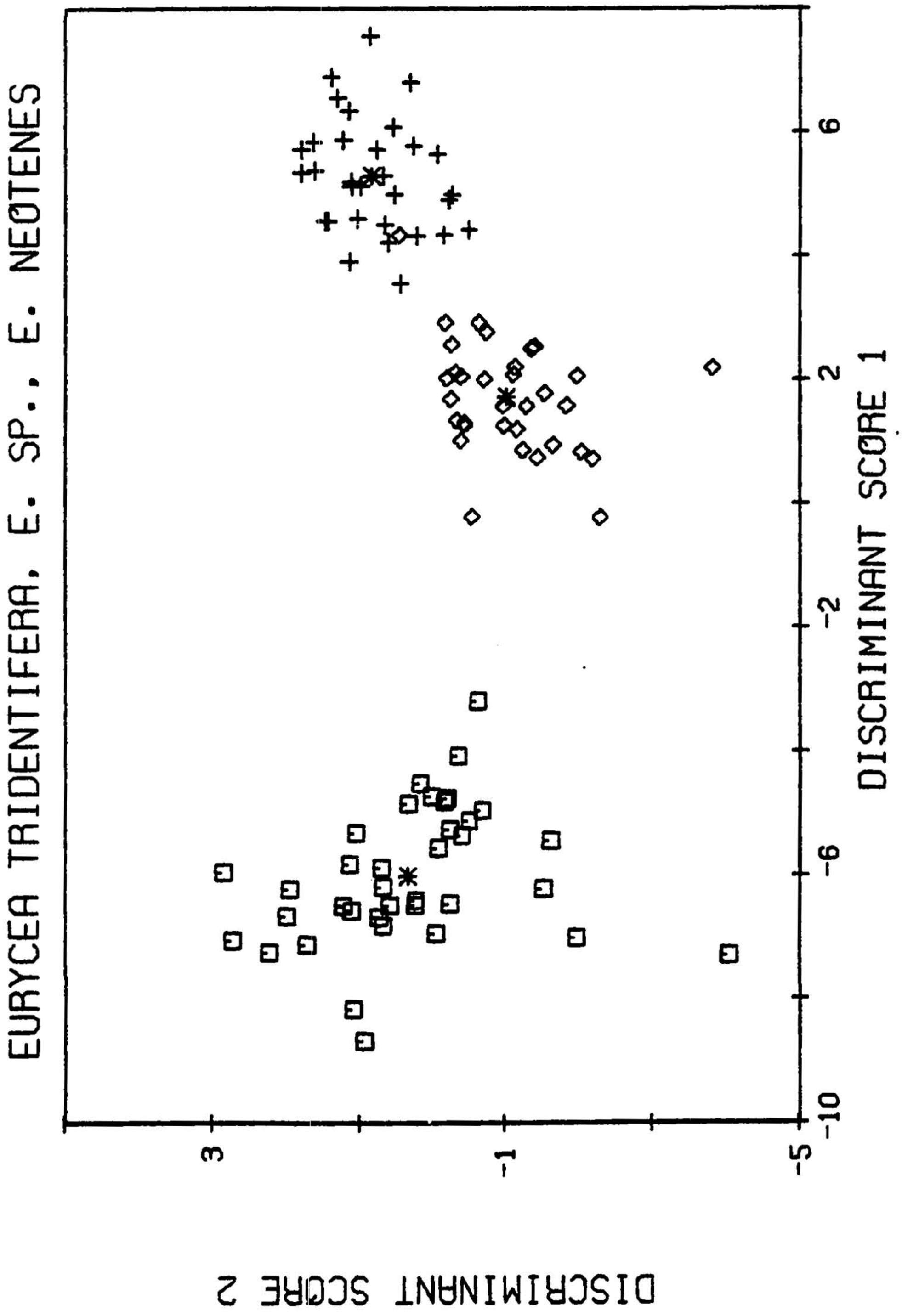

EURYCEA TRIDENTIFERA, E. LATITANS, E. NEOTENES
DISCRIMINANT SCORE 2
4
2
0
-2
-4
-10
-6
-2
2
6
DISCRIMINANT SCORE 1

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


EURYCEA TRIDENTIFERA, E. SP., E. NEOTENES
DISCRIMINANT SCORE 1
DISCRIMINANT SCORE 2
-10
-6
-2
2
6
3
-1
-5

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

By the specification of the reference groups alone, the individuals constituting the intermediate samples can be forced to assort on the basis of the simple majority of their affinity. In this analysis three intermediates from Honey Creek Cave sort with *E. neotenes* and one with *E. tridentifera*. This majority is also reflected in the forced assortment of the *E. troglodytes* sample: 27 specimens are aligned with *E. neotenes*, and 11 with *E. tridentifera*. All but two of the 17 *E. latitans* sort with *E. neotenes*. As a further step, the samples of *E. troglodytes* and *E. latitans* can be divided into three and two groups, respectively, on the basis of collection date to evaluate the possibility that these populations have changed in composition during the past few decades. When this is done with the *E. troglodytes* sample, a clear trend towards the influence of *E. neotenes* emerges in the ratio of forced assortment of *E. tridentifera*:*E. neotenes* as follows: 1957, 7:8; 1967, 2:4; 1972-1974, 1:13. Three specimens of unknown collection date are omitted. Using the results of the three-group discrimination, the distributions of each of these subgroups in discriminant space can be compared by multivariate analysis of variance. These tests show that the shift seen in the 1972-1974 subgroup represents a significant departure ($p < 0.01$) from the distributions of the two earlier subgroups. The 1957 and 1967 subsamples do not differ from one another significantly. The four E. troglodytes misclassified in the three-group analysis consist of two from the 1957 subgroup and one from the 1967 subgroup having higher posterior probabilities of assortment with E. tridentifera than with E. troglodytes, and one specimen from the 1972-1974 subgroup which is aligned with E. neotenes.

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

The general outcome of these tests is that the three suspected hybrid samples presently share greater affinity with E. neotenes than with E. tridentifera. In both cases where temporal subdivision of the samples is possible, individuals aligned with E. tridentifera strongly predominate in the early collections, amounting to 9 of the 12 so assorted in the two-group tests, and four of the five misclassified in the three-group analyses. Because early samples comprise about half of the available material in each case, the observed trend is probably not an effect of disparate sample sizes.

### Character Discordance

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

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

Two general limitations of the technique apply to morphological data: the independent variable should be the same for all characters employed, and the distribution of cases should be ordinal or otherwise uniform in nature. Size is the obvious independent variable in most applications at the population level, although the suite of characters comprising an adaptive trend could be employed in a comparison among taxa. In the present application each specimen in a sample is assigned a rank for each of the seven size-dependent characters previously used; trunk vertebral number is not correlated with ontogenetic size change and has been omitted. In a perfectly concordant sample each specimen would have a consistent, uniform rank across the set of characters. As the degree of size dependence of character states diminishes, heterogeneity will appear in the individual rank scores, reducing the concordance value of the sample. Used in this way, the concordance value is essentially a measure of the degree of homogeneity among the allometric relationships of the variables within a sample of specimens. Populations having a uniform set of allometric relationships will be more nearly concordant than will those in which sets from different parental taxa are variously recombined.

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

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

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

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

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

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

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

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

## Reproductive Condition

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

The sex ratio is equal in the Honey Creek Cave sample, but males predominate in both *E. troglodytes* (14:9) and *E. latitans* (14:6); neither distribution deviates significantly from equality by chi-square test. The predominance of males (17:3) reported in the type series of *E. latitans* (Smith and Potter, 1946) together with sexed specimens from later collections (total, 30:5) represents a significant deviation from a 1:1 ratio. The data from the type series are not entirely reliable,as Brandon (1971) has shown that the sex of the holotype was incorrectly determined. The six individuals from this series which have been sexed by internal examination are included in the first-mentioned sex ratio. Apart from this possible imbalance, E. troglodytes and E. latitans are apparently reproductively competent; together with the Honey Creek Cave intermediates, individuals of these populations reach large size and generally contain large fat bodies as well as gonads of normal morphology.

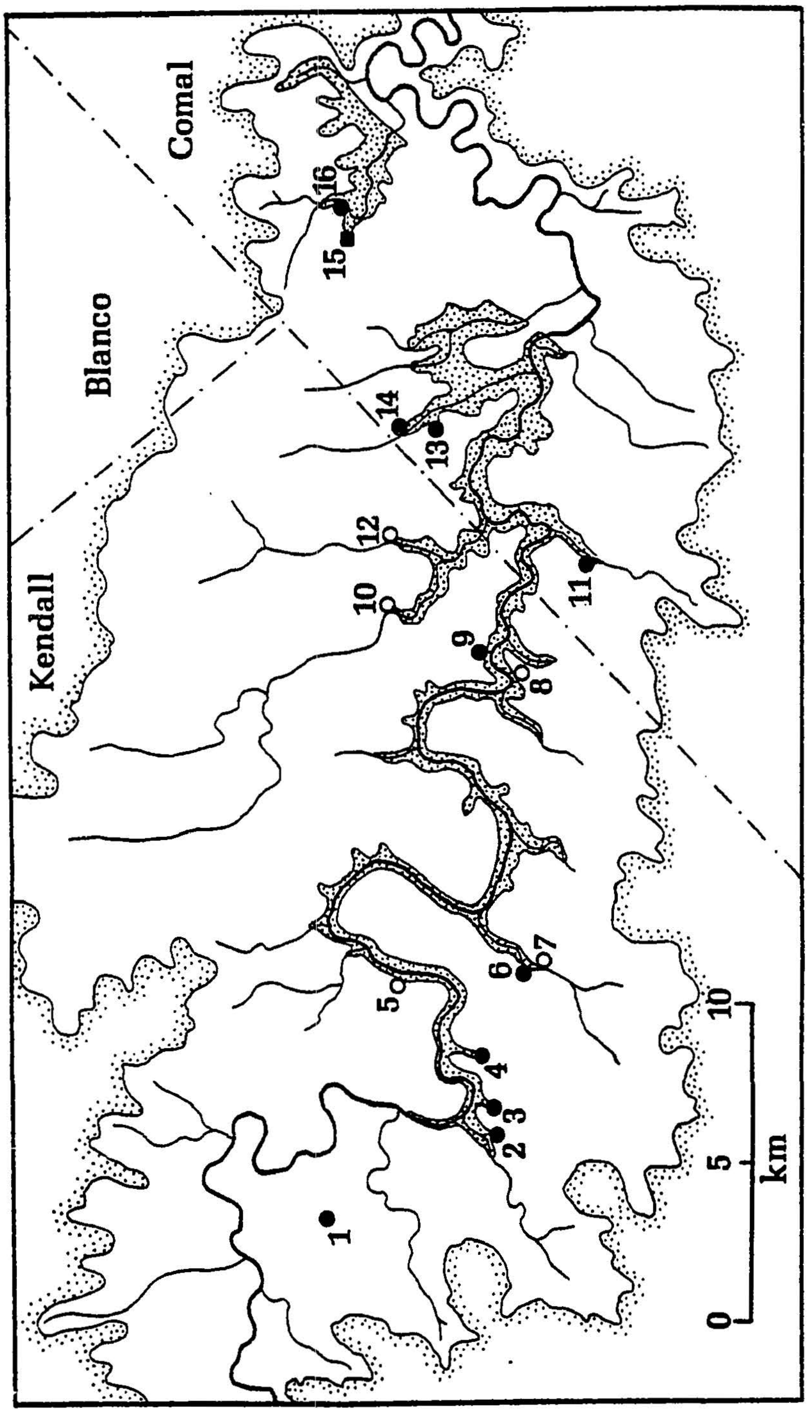
## Discussion

### Possible Competitive Exclusion at Honey Creek Cave

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

As noted in Chapter II the entrenchment of the Guadalupe River in Kendall and western Comal counties has resulted in the development of numerous local subterranean drainages. The incised river bed now lies 50-110 m below the surface of its broad Pleistocene valley (George, 1952), which has an area of about 700 square kilometers (Fig.31). Surface drainages and springs are poorly developed on the valley floor and tend to be intermittent upstream from their short ravines bordering the river; consequently, epigean populations of Eurycea are infrequent on the valley floor (Chapter IV). The valley surface is developed on the hard and lithically uniform but soluble lower member of the Glen Rose Limestone, which is underlain by the clayey dolomites and sandstones of the Hensel Sand (Stricklin, Smith and Lozo, 1971). The Hensel is resistant to solutional erosion, and its upper surface forms a base level for the cave systems of the middle Guadalupe valley, which originate in sinkholes on the valley surface and drain towards the river canyon (Smith, 1971). These systems span a broad range in size and complexity, from linear passages $<$ 200 m in length with one to several local sinkholes (sites 2,3,8,9 and 12; Fig. 31), to large branching drainages $>$500 m in length, which receive surface runoff through a large number of sinkholes (sites 6,7,13 and 14). Most of these subterranean drainages open into the heads of tributary ravines, and all but one occur at the contact between the Hensel Sand and the overlying lower Glen Rose Limestone (Smith, 1971; Fig. 31); site 16 is a small cave developed in the Cow Creek limestone underlying the Hensel Sand. Water emerges from either the cave entrance or from adjacent rock rubble in sites 2-14 and 16; site 1 is a sinkhole tributary of a presently unlocated spring, and site 15 is a spring lacking an associated cave. Most of these outlets, as reported by local landowners, flow permanently (George, 1952; Reeves, 1967), and most of them appear to provide suitable

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


Kendall
Blanco
Comal
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
0
5
10
km

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

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

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

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

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

32.

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

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

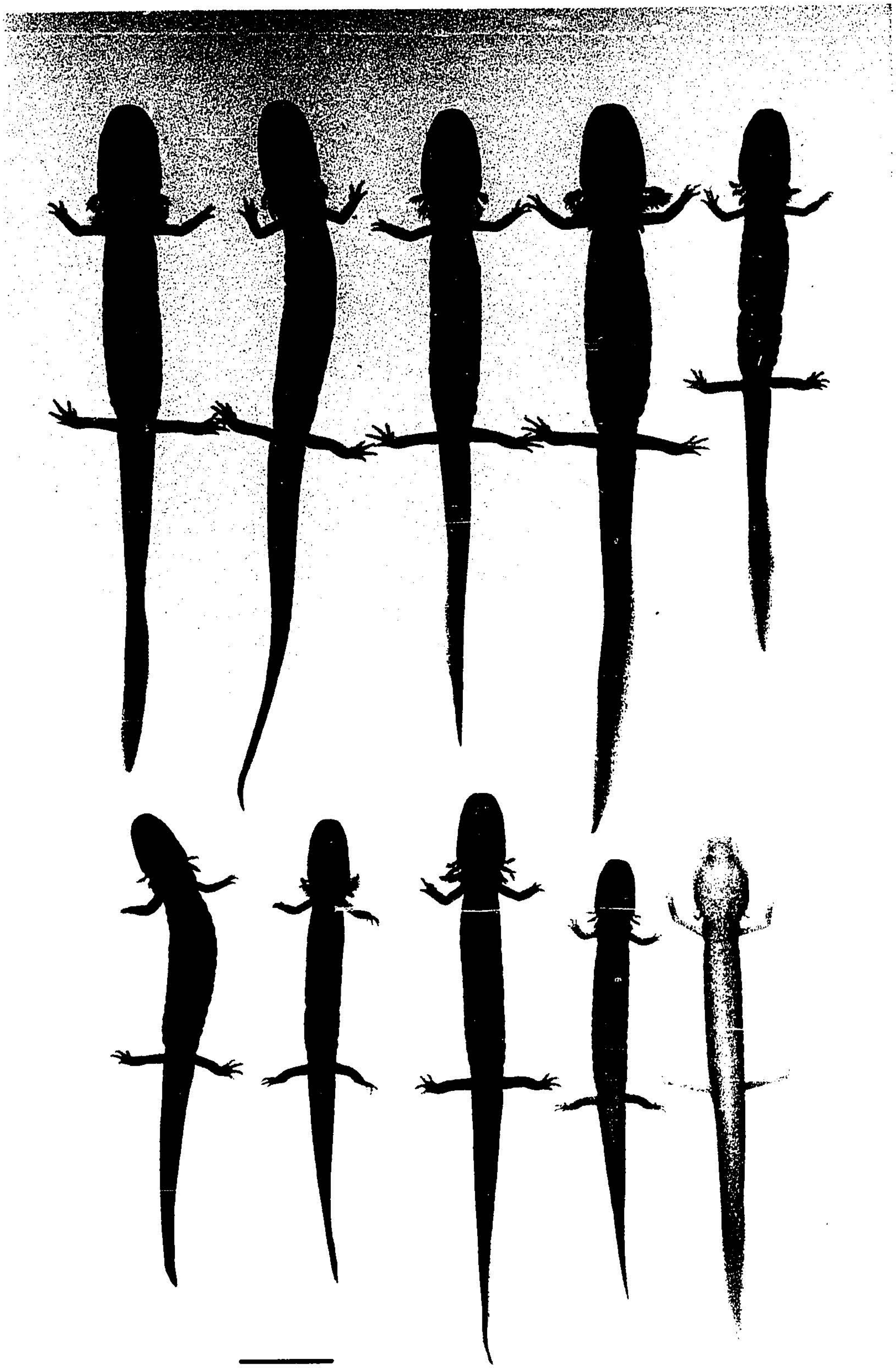
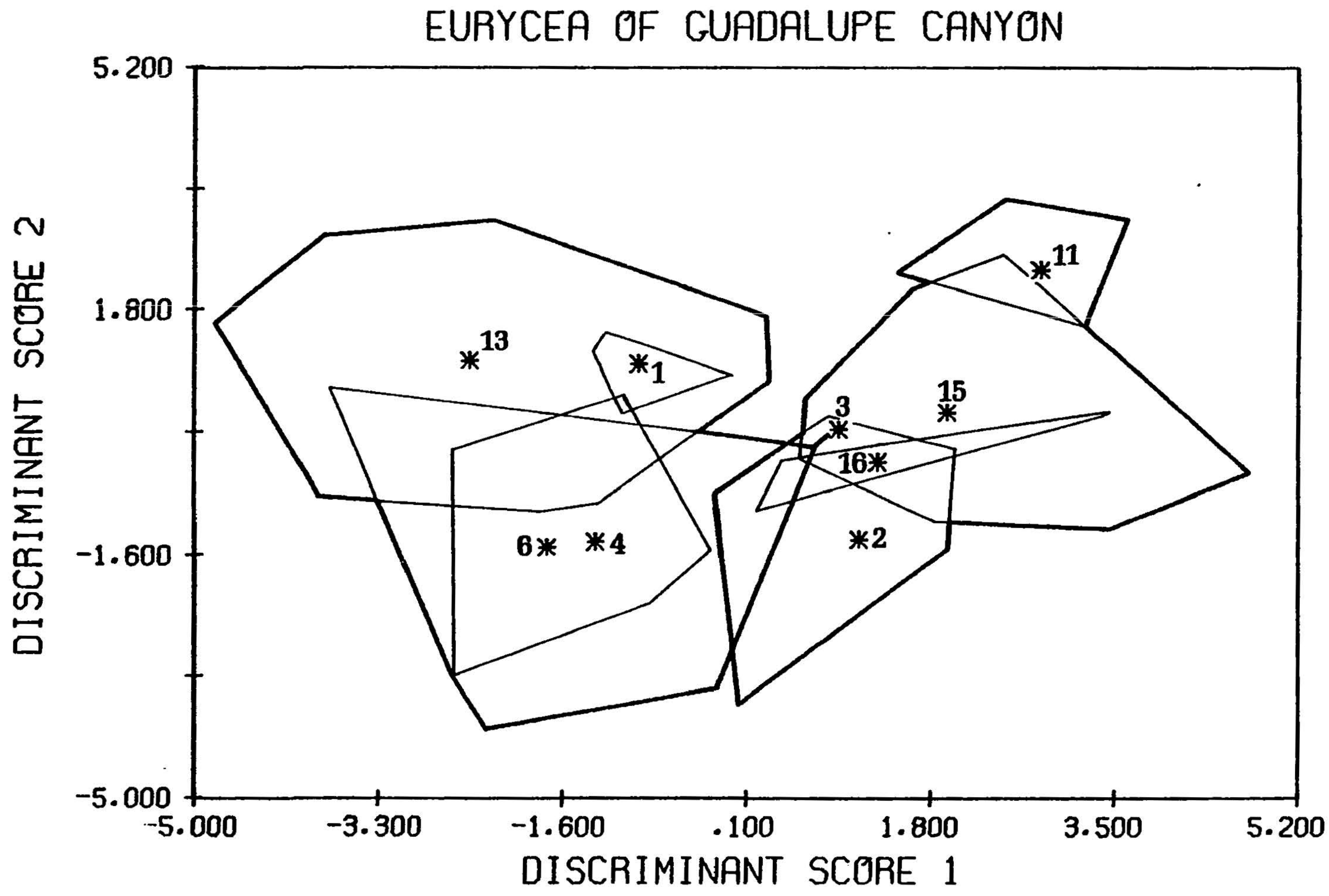


Table 17. Standardized character coefficients for 9 and 2 group discriminant analyses of *Eurycea neotenes* from the Guadalupe River canyon, Comal and Kendall Counties, Texas.

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

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


EURYCEA OF GUADALUPE CANYON
5.200
1.800
-1.600
-5.000
DISCRIMINANT SCORE 2
-5.000
-3.300
-1.600
.100
1.800
3.500
5.200
DISCRIMINANT SCORE 1
13
1
6
4
3
15
16
2
11

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

From an inspection of Figure 33 it is clear that the epigean and troglobitic subgroups exist in discriminant space. Group membership is unrelated to the location of sites along the river. Within the epigean subgroup the relative positions of three of the four populations correspond exactly with the frequency of occurrence of individuals in the cave environment. The sample from Victor Phillip Water Cave (site 2) bridges the epigean and troglobitic subgroups and is the only population in which specimens are frequently found in the cave as well as on the surface. Rebbecca Creek Spring (site 16) issues from a small cave, of which only a few meters are accessible owing to an artificial dam at the entrance. One salamander was seen, but not collected, above this dam on one of three visits. Puter Creek spring (site 15), where no cave is evident, issues from gravel in a streambed at the Hensel-Glen Rose contact; the sample from this site has relatively high values on both discriminant axes, exceeded only by the Honey Creek Cave E. neotenes. The Honey Creek population seems at first sight to contradict this trend. It is the most distinct of the epigean populations, yet the spring in which it occurs emerges directly from a large cave, and one specimen was collected about 25 m inside the entrance (Mitchell and Reddell, 1965). When these findings are placed in conjunction with the knowledge that *E. tridentifera* occupies Honey Creek Cave the apparent anomaly can be reversed by accepting the interpretation that competitive exclusion of *E. neotenes* by *E. tridentifera* has taken place. My interpretation is that *E. neotenes* fails to show the expected moderate degree of troglobitic adaptation owing to selection against individuals in the subterranean adaptive zone, where a different, highly specialized troglobitic population is established. These data might be further interpreted as indicating character displacement, if only local populations of *E. neotenes* are considered. A broader view suggests that this is not the case, in that neither of these sympatric populations differs in a substantive way from other populations of their respective taxa.

The sequence of colonization in Honey Creek Cave is unclear. Distributional evidence suggests that *E. tridentifera* has entered the Guadalupe region from the Cibolo sinkhole plain to the south, where the majority of populations occur, whereas *E. neotenes* has probably long occupied this area. The development of cave systems probably began prior to the entrenchment of the Guadalupe River, as is presently the case along Cibolo Creek, but three lines of evidence suggest that large regional cave systems such as occur to the south did not form during this period. Unlike the Cibolo system, the middle Guadalupe drainage is distant from the Balcones Fault Zone aquifer. In the absence of the strong hydrologic gradient this proximity provides, the movement of groundwater through developing cave systems was probably slow prior to the entrenchment of the river, at which time a strong potential gradient developed. A low groundwater divide presently exists between the Guadalupe and Cibolo drainages (George, 1952; Reeves, 1967), and there is no evidence that any of the caves of the Guadalupe region are tributaries of the Cibolo system. The size and form of the Guadalupe caves provides a second point of evidence. Most are relatively small, and none is known to be connected, as might be expected if a large regional system had been transected by the developing river canyon. Two caves (sites 7 and 11) bifurcate near their present entrances, and both passages are approximately equal in size. These distributaries did not develop until the cave was breached by erosion, and their equal sizes suggest that the caves which existed prior to entrenchment were small (W.H. Russell, personal communication, 1974). The third point is simply that E. tridentifera occupies only one of the Guadalupe caves, contrary to an expected broader distribution if regional systems were developed.

Populations of E. neotenes probably occupied the developing springs at a relatively early date, perhaps prior to the arrival of E. tridentifera, but there is little evidence to indicate when colonization of caves by epigean populations began. This process is apparently still occurring, both in the Guadalupe region and elsewhere on the Edwards Plateau (Sweet, 1977a [Chapter V] ). It is parsimonious to assume that *E. tridentifera* antedates the events which would lead to colonization of Honey Creek Cave by *E. neotenes*, rather than proposing a more complex model involving the extirpation or exclusion of an existing troglobitic population of *E. neotenes*.

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

There may be evidence of competitive displacement in the overall pattern of distribution of *E. neotenes* and *E. tridentifera* as well as in the local situation at Honey Creek Cave. Each of the instances of secondary contact demonstrated or inferred here is peripheral to the distribution of *E. tridentifera*; the latter is enclosed within the range of *E. neotenes*. Surface dwelling populations of the latter are uncommon within the region occupied by *E. tridentifera*, probably because the geologic conditions producing extensive subterranean drainages generally preclude the existence of reliable springs. Troglobitic populations of *E. neotenes* are apparently absent from the main range of *E. tridentifera* on the Cibolo sinkhole plain. This is the only well-surveyed cave region in the range of *E. neotenes* lacking such populations, a distinction suggesting that the presence of the advanced troglobite has prevented subsequent colonization on a regional scale.

## Conclusion

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

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

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

A degree of reproductive isolation appears to be in effect at Honey Creek Cave; this may result from either the existence of isolating mechanisms, or very infrequent contact of the two populations across the gradient separating cave from surface habitats. While the latter distinction is of great importance in explaining the presence of *E. neotenes*, it seems unlikely that habitat preferences alone would be effective in isolating the two genomes over an extended period. These populations would be expected to be competitively superior in their respective habitats (see, for example, Poulson and White, 1969), empowering selection against hybridization and hence for the origin of reproductive isolation. The comparatively low concordance value of Honey Creek Cave *E. tridentifera* may reflect the movement of hybrid individuals into the population in the past, but on the whole these populations remain distinct.

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

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

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

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

Several caves in the Guadalupe canyon and along Cibolo Creek regularly contain a variety of fishes introduced during periods of flooding (Reddell, 1967b, 1971; and personal observations). These fish apparently survive for appreciable periods, and include such potentially predatory genera as *Ictalurus*, *Lepomis* and *Micropterus*; however, there is presently no direct evidence that troglobitic *Eurycea* are consumed in these situations. Nonetheless, with the exception of the Cascade Caverns-Cascade Sinkhole system (site 2 of Fig. 23), caves with fish are without populations of *Eurycea*, though some (such as Prassell Ranch Cave and Spring Creek Cave in the Guadalupe canyon, sites 5 and 7 of Fig. 31) are apparently otherwise suitable, and are bracketted by fish-free caves inhabited by *Eurycea* (Fig. 31). *Eurycea latitans* coexists with *Lepomis* spp., including *L. cyanellus*, and *Micropterus* spp. in Cascade Sinkhole. Most of the salamanders occur in pools too small to support fish, but a few have been observed in piles of cobble and plant debris in the larger pools (A.G. Grubbs, personal communication, 1976). The Cascade system appears to contain more deposits of gravel and cobble than other caves in the region, which may permit the persistence of *Eurycea* in the presence of fish.

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

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

In conclusion, I suggest that the observed interactions are consistent with the interpretation that *E. neotenes* and *E. tridentifera* are closely related but distinct species. *Eurycea troglodytes* Baker, 1957, consists of a hybrid swarm and is thus an invalid taxon which is here placed in the synonymy of *E. neotenes* Bishop and Wright, 1937 (part) and *E. tridentifera* Mitchell and Reddell, 1965 (part). Continued recognition of *E. latitans* is probably unwarranted, as its distinctive characteristics could easily result from limited hybridization. Were it not for the extreme variation observed in vertebral number this population would be morphologically indistinguishable from most of the independent and parallel troglobitic populations of *E. neotenes* which occur widely on the Edwards Plateau. Accordingly, I suggest that the name *E. latitans* Smith and Potter, 1946, be regarded as a junior synonym of *E. neotenes* Bishop and Wright, 1937 (see also Chapter IV).

## Summary

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

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

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# CHAPTER VII

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

## Introduction

Names applied to questionable taxa with restricted geographic distributions or of rare occurrence tend to have considerable inertia in the literature, and often persist without reevaluation well beyond the emergence of a general consensus on their validity, primarily as a result of the scarcity of preserved material. Exclusively allopatric taxa compound this problem, in that series representative of the range of variation in related populations must be at hand before meaningful evaluation of the taxonomic status of a described form can take place. Most of these problem criteria are met by the paedogenetic plethodontid salamanders of the Edwards Plateau of central Texas. The Fern Bank salamander, *Eurycea pterophila* Burger, Smith and Potter (Burger *et al*., 1950) has generally been accorded species status by workers with some familiarity with the diversity of the Texas *Eurycea* (Baker, 1957, 1961; Blair, 1957; Potter and Rabb, 1960; Mitchell and Reddell, 1965; Wake, 1966; Bogart, 1967; Mitchell and Smith, 1972), though there have long been serious doubts about its validity. With increasing frequency authors have relegated *E. pterophila* to subspecific status within *Eurycea neotenes* (e.g., Schmidt, 1953; Conant, 1958, 1975; Brame, 1967; Raun and Gehlbach, 1972; Hamilton, 1973), but only Brown (1967) has published a brief statement in justification for this course of action. Hendricks (1973) is the first author to suggest that *E. pterophila* should be denied nomenclatural status; the taxon is not listed in a recent checklist by Thomas (1974), and is the only named form of *Eurycea* of restricted distribution not protected as rare or endangered by Texas state law. The trend away from recognition of *E. pterophila* in recent herpetological literature is clear, but there remains scant evidence for this conclusion.

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

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

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

## Material

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

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

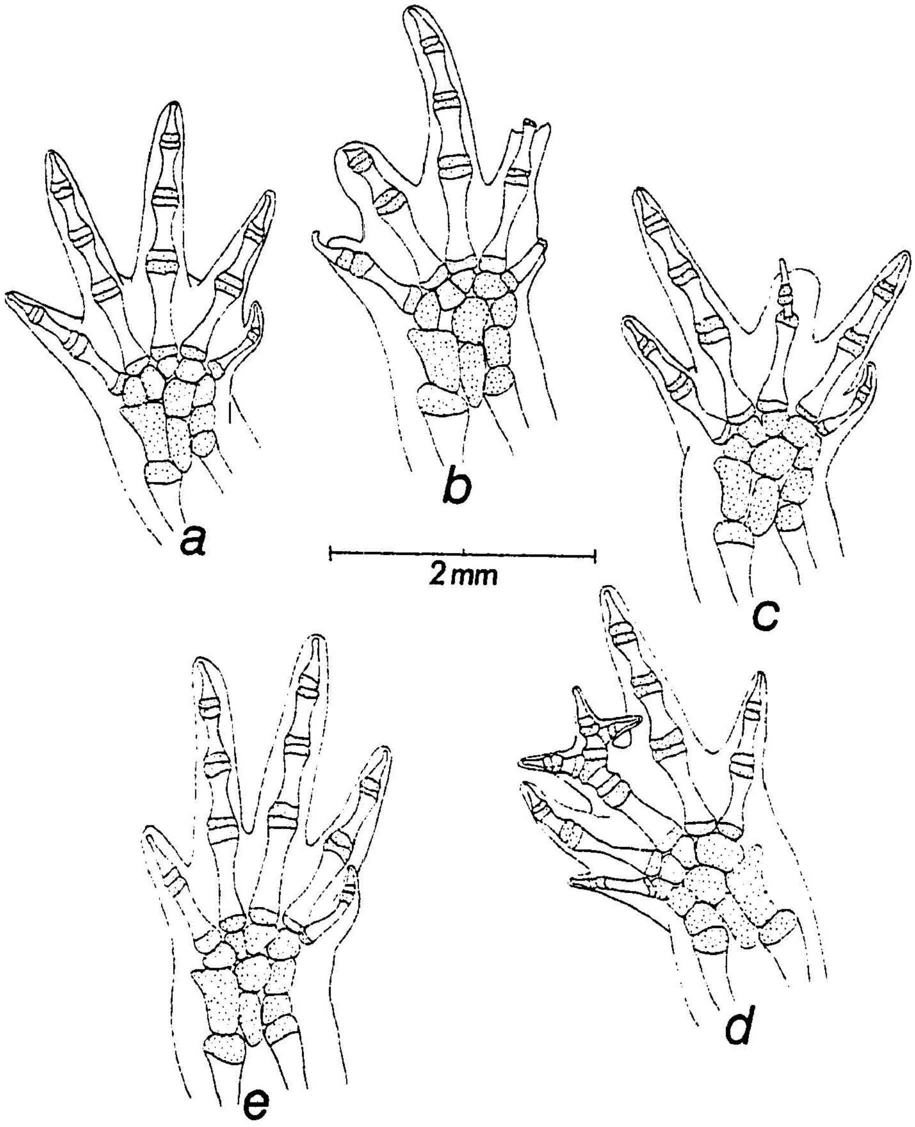
## Results

### Phalangeal Reduction

From Table 1 of Burger *et al*. (1950: p. 53) it is evident that their term "phalanges" includes the metapodial elements as well as phalanges; the term is herein employed in its usual sense. The Texas Eurycea have phalangeal formulae of 1-2-3-2 (forelimb) and 1-2-3-3-2 or 1-2-3-3-1 (hindlimb). Inspection of Fig. 34 suggests that the phalangeal reductions observed in E. pterophila are primarily pathological in nature, involving the loss of terminal phalanges or whole digits long after their differentiation and growth, rather than some regular pattern of reduction in phalangeal formula as is frequently seen in other tetrapods. The lack of anatomical modification of the tips of the reduced digits and their frequent protrusion from the skin, together with the frequent presence of proximal fragments of the missing phalanges strongly suggests that these elements were lost by action of mechanical injury or disease subsequent to the development of a normal phalangeal complement. Further evidence for this view may be adduced from the frequent occurrence of regenerating digits of normal and abnormal morphology (Fig. 34 ). Although difficult to document in a definitive fashion, the location and structure of the digital deformities bear close resemblance to the effects of redleg (Aeromonas sp.) infection (Reichenbach-Klinke and Elkan, 1965). This disease in Eurycea results in part in localized necrosis which often removes only parts of bony elements; subsequent regeneration is more frequently abnormal than is regeneration from mechanical injury.

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

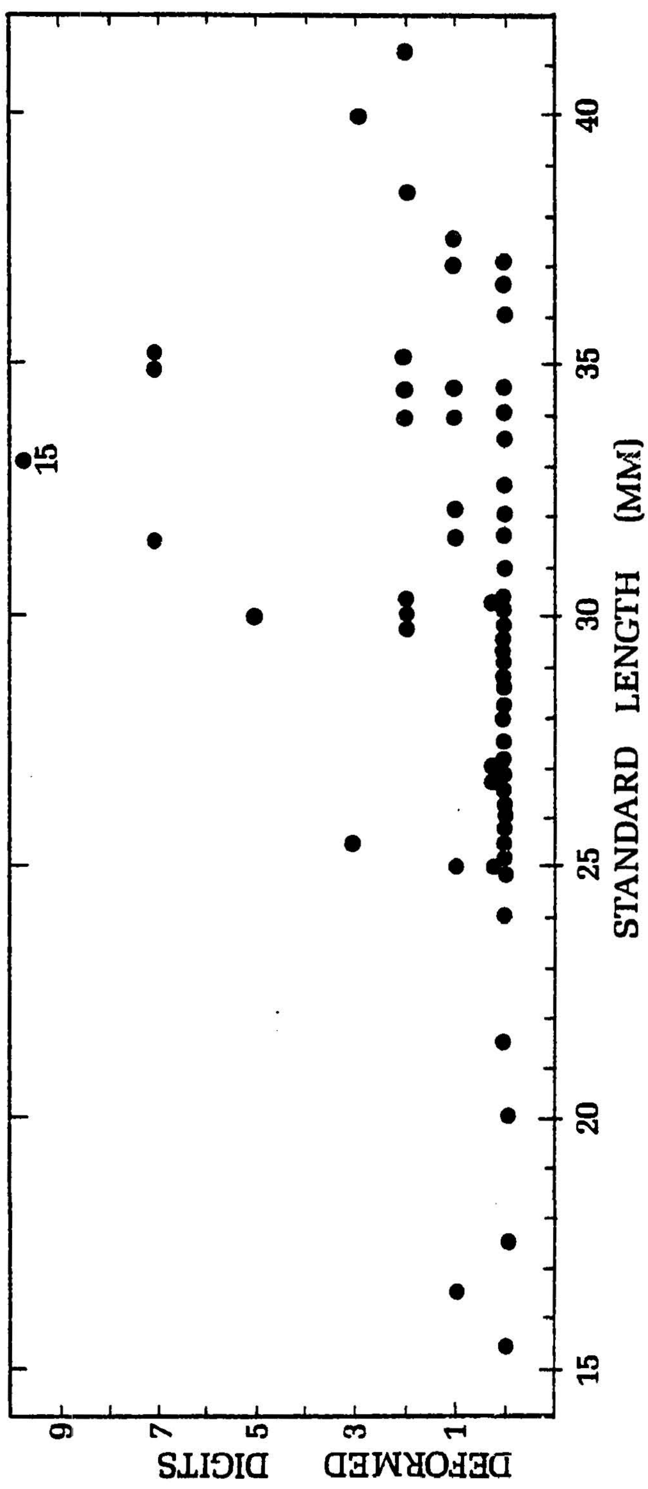
Figure 34. Hind feet of 5 specimens of Eurycea pterophila, drawn from cleared and stained specimens. Cartilage is stippled; a,b,c, and e represent left feet. The figure shows; (a) normal tarsal, metatarsal and phalangeal complement (MVZ 120936); (b) digits deformed by mechanical injury or disease; note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


a
b
c
d
e
2mm

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

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

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


DEFORMED DIGITS
9
7
5
3
1
STANDARD LENGTH (MM)
15
20
25
30
35
40
15

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

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

### Sacral and Presacral Ribs

The proportions of the sacral and presacral ribs are variable in the Texas *Eurycea* both in ontogeny and among populations. The "presacral" ribs figured by Burger *et al.* (1950, Plate VI) apparently include the sacral rib as well, denoted as "presacral #1"; statements in the text in reference to the last rib also pertain to the sacral rib, and their "penultimate rib" is thus that of the presacral vertebra. As far as can be determined from the available cleared and stained ontogenetic series of *E. nana* and *E. neotenes* the pattern of rib development in the Texas *Eurycea* is similar to that described for *Eurycea bislineata* by Wake and Lawson (1973). The ventral rib head ossifies prior to the appearance of ossification in the dorsal head; the dorsal head is not preformed in cartilage on the posterior trunk vertebrae, but does so appear in the sacral rib. The dorsal head of the sacral and presacral ribs ossifies from the shaft dorsomedially to join the dorsal rib bearer. This process is comparatively rapid in the sacral rib, which is bicipital in *E. pterophila* as small as 25 mm in standard length. The dorsal head of the presacral rib ossifies more slowly or not at all, remaining unicipital in some cases.

The sacral rib is stated to be unicipital in *E. pterophila*. Examination of the figures provided (Burger *et al*., 1950, Plate VI, D and E) shows the sacral rib in these specimens to have both heads, which are simply fused together by bony growth in the interhead region, rather than being truly unicipital. In 27 cleared and stained *E. pterophila* both fully bicipital and fused bicipital conditions occur: categorization of this variation is difficult, and asymmetry is common. Of 54 sacral ribs examined, 29 are strongly bicipital (heads separated by a gap at least as deep as either head is wide), and 14 are fully fused (with no interhead concavity); the remainder are of intermediate form. The morphology of the articulation of the sacral rib is thus not a constant character as represented in *E. pterophila*. As is the case within the topotypic series, sacral rib form is quite variable in and among other populations of the Texas *Eurycea*. The most frequent pattern consists of predominantly bicipital ribs, with occasional secondary fusions as seen in *E. pterophila*. Some populations show near constancy in sacral rib form, as follows. All examined specimens (seven) from Henderson Branch Creek, Kerr County, have fused rib heads, as do the specimens (three) from Salamander Cave, Travis County. The sacral rib is bicipital in all 16 specimens from Mill Creek, Bandera County. In the remaining populations examined, including topotypic *E. neotenes* and specimens from five other localities, as well as in *E. nana*, *E. latitans*, *Eurycea troglodytes* and *Eurycea tridentifera*, most sacral ribs are bicipital, but all populations show the fused condition in at least one individual. Accordingly, by virtue of variation in the topotypic population and corresponding variation in all other species of Texas *Eurycea*, the morphology of the sacral rib is judged to be an inadequate character on which to differentiate the Fern Bank Spring population.

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

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

### Urohyal Form and Ossification

There are several errors in the representation of the hyobranchial apparatus of species of Texas Eurycea figured by Burger et al. (1950, Plate VII), the most significant for this discussion being two: the failure to show the cartilaginous stylus which connects the urohyal to the remainder of the hyobranchial apparatus; and the failure to illustrate the form of the cartilaginous processes of the urohyal posterior to the illustrated ossification centers. The urohyal is continuous with the hyobranchial apparatus proper in all larval hemidactyliine plethodontids (Wake, 1966), and the cartilaginous anlage of the urohyal is triradiate (with occasional exceptions) in all, though it is variably mineralized or ossified. The urohyal and its stylus are preformed in cartilage early in larval life; the lateral rami of the urohyal provide an insertion site for the rectus cervicis superficialis and hebosteoypsiloideus musculature from the ventral surface of the unit. The median ramus lies in the midventral raphe, where it is continuous with the connective tissues of the linea alba. The degree of ossification of the urohyal is size related, and is consistent with a stress response to the mechanics of gape-and-suck feeding; the lateral rami generally are bridged by bone across the body of the element in an irregularly Y-shaped configuration prior to the ossification of the median ramus.

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

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

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

## Conclusion

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

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# CHAPTER VIII

# CONCLUSION:

# THE DEVELOPMENT OF DIVERSITY IN THE TEXAS EURYCEA

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

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

The distributional connection between the Interior

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

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

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

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

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

As springs fail through erosion of the land surface and the resultant lowering of the local water table, resident populations must either spend increasing amounts of time underground or disappear. In this way troglobitic populations originate by gradual adaptation to subterranean life; paedogenesis represents a coincident adaptation in this context. The local nature of this process ensures that cave populations originate independently, and at locally determined rates and times. The entire sequence of preadaptation to and colonization of caves (which are the drainage networks discharged by springs) thus proceeds in a parallel fashion, and fully satisfies the design criteria for a replicated natural experiment. Of the 26 known troglobitic populations of *Eurycea*, 13 clearly represent independent colonizations by populations of *E. neotenes*; another seven populations are very likely to be independently derived. The six remaining populations (of the advanced troglobite *Eurycea tridentifera*) appear to represent subterranean dispersal of a single ancestral population.

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

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

Major assistance in setting a base level for the degree of evolutionary divergence among populations of the Texas _Eurycea_ is provided by three apparent cases of secondary contact involving _E_. _neotenes_ and _E_. _tridentifera_. Actual sympatry between the two species is documented only at Honey Creek Cave; the interactions in the Cascade Caverns System and Valdina Farms Sinkhole are inferred from the characteristics of the resident populations. The opportunity for ecological isolation between epigean and troglobitic populations is present at Honey Creek Cave, and here _E_. _neotenes_ and _E_. _tridentifera_ interact as species. Only four of 70 specimens from this site are hybrids. There is some evidence from a comparison of the other populations of *E. neotenes* of the middle Guadalupe valley that *E. neotenes* at Honey Creek Cave has been competitively excluded from the cave environment by *E. tridentifera*.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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# Appendix I

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

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

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

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

<u>Bandera County</u>

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Bell County

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

Bexar County

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

Bexar County concl.

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

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

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

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

Blanco County

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

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

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

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

Comal County

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

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

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

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

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

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

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

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

Edwards County

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

Edwards County concl.

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

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

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

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

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

Hays County

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

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

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

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

Kendall County

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

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

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

Balcones Creek spring, 1470': 29$^{\circ}$ 44' 18" N, 98$^{\circ}$ 44' 27" W; 3.2 mi. SSW Boerne. M.V.Z. 121228.

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

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

Kerr County

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

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

176 Spring, 1870': 30° 05' 18" N, 99° 19' 14" W; 1.6 mi. NNE Hunt. T.C.W.C. CS-108 - CS-112; M.V.Z. 121405-121466.

Unnamed creek spring, 1860': 30° 01' 00" N, 99° 21' 06" W; 4.0 mi. S Hunt. M.V.Z. 121524-121543.

Fessenden Branch spring, 1890': 30° 09' 58" N, 99° 21' 03" W; 1.7 mi. SE Mountain Home. M.V.Z. 121467-121484.

Honey Creek spring, 1900': 30° 06' 02" N, 99° 21' 42" W; 2.8 mi. NW Hunt. M.V.Z. 121485-121586.

North Fork Guadalupe River spring, 1880': 30° 03' 04" N, 99° 26' 54" W; 7.1 mi. WSW Hunt. M.V.Z. 121487.

Lange Ravine east spring, 1860': 30° 01' 57" N, 99° 23' 05" W; 3.9 mi. SW Hunt. M.V.Z. 121488-121522.

Lange Ravine west spring, 1860': 30° 01' 57" N, 99° 23' 07" W; 4.0 mi. SW Hunt. M.V.Z. 121423.

Edmunson Creek east spring, 1900': 30° 00' 23" N, 99° 21' 44" W; 5.8 mi. SSW Hunt. M.V.Z. 121544-121558.

Edmunson Creek west spring, 1880': 30° 00' 21" N, 99° 21' 54" W; 5.8 mi. SSW Hunt. M.V.Z. 121559-121561.

Buffalo Creek spring, 1900': 29° 58' 18" N, 99° 22' 35" W; 6.5 mi. SW Hunt. M.V.Z. 121562-121583.

Chimney Spring, 1884': 30° 00' 19" N, 99° 24' 25" W; 6.2

### Kerr Co. concl.

mi. SW Hunt. M.V.Z. 121584-121594.

Cherry Creek spring, 1910': 30° 00' 34" N, 99° 24' 38" W; 6.3 mi. SW Hunt. M.V.Z. 121595-121617.

Fall Creek spring, 1910': 29° 54' 45" N, 97° 12' 20" W; 9.6 mi. SSW Kerrville. M.V.Z. 121670-121894.

Lambs Creek spring, 1900': 29° 55' 20" N, 99° 14' 21" W; 10.6 mi. SW Kerrville. M.V.Z. 121895-122831.

Turtle Creek spring, 1980': 29° 59' 06" N, 99° 15' 51" W; 8.0 mi. SW Kerrville. M.V.Z. 121617-121669.

Robinson Creek spring, 1840': 29° 54' 55" N, 99° 15' 08" W; 8.1 mi. NNW Medina (Bandera Co.). M.V.Z. 122078-122090.

Wallace Creek spring, 1700': 29° 54' 48" N, 99° 17' 52" W; 8.7 mi. NNW Medina (Bandera Co.). M.V.Z. 122091-122093.

### Medina County

Seco Creek spring, 1310': 29° 35' 17" N, 99° 23' 58" W; 2.8 mi. SSE jct. Bandera, Medina and Uvalde cos. M.V.Z. 122125-122129.

Richter Springs, 1400': 29° 35' 32" N, 99° 23' 07" W; 9.4 mi. SE Utopia (Uvalde Co.). M.V.Z. 122094.

New Pump Spring, 1580': 29° 36' 14" N, 99° 21' 42" W; 10.4 mi. ESE Utopia (Uvalde Co.). M.V.Z. 122095-122108.

Yellow Spring, 1525': 29° 36' 56" N, 99° 22' 05" W; 10.7

Medina County concl.

mi. E Utopia (Uvalde Co.). M.V.Z. 122109-122124.

Real County

West Sabinal River tributary spring, 1620': 29° 41' 13" N, 99° 37' 22" W; 7.6 mi. NW Utopia (Uvalde Co.). T.N.H.C. 21669 (17 specimens); 21670.

Harris Spring, 1640': 29° 43' 24" N, 99° 37' 10" W; 9.2 mi. NW Utopia (Uvalde Co.). T.N.H.C. 21674 (40 specimens).

Ash Hollow spring, 1840': 29° 44' 07" N, 99° 38' 37" W; 8.4 mi. ENE Leadey. M.V.Z. 122142-122364.

Mud Spring, 1910': 29° 40' 30" N, 99° 40' 02" W; 5.0 mi. NE Rio Frio. M.V.Z. 122377-122398.

Little Dry Frio Creek tributary spring, 1800': 29° 43' 12" N, 99° 40' 10" W; 7.0 mi. E Leakey. M.V.Z. 122365-122376.

South Prong Cypress Creek north spring, 1830': 29° 47' 58" N, 99° 38' 54" W; 9.3 mi. NE Leakey. M.V.Z. 122399-122407.

South Prong Cypress Creek south spring, 1910': 29° 47' 46" N, 99° 39' 58" W; 9.2 mi. NE Leakey. T.C.W.C. CS-149 - CS-150; M.V.Z. 122408-122476; 122832.

East Frio River spring, 1850': 29° 51' 02" N, 99° 40' 02" W; 11.6 mi. NE Leakey. M.V.Z. 122477-122587.

Bee Cave Hollow spring, 2030': 29° 54' 25" N, 99° 47' 27" W; 11.0 mi. N Leakey. M.V.Z. 122592-122671.

Real County concl.

Short Prong Frio River spring, 2000': 29° 55' 00" N, 99° 47' 30" W; 12.0 mi. N Leakey. M.V.Z. 122588-122591.

Prade Ranch spring, 1950': 29° 54' 51" N, 99° 47' 02" W; 12.0 mi. N Leakey. F.M.N.H. 55086 (2 specimens); 55087-55090; 55092-55093; 55095-55096.

Old Faithful Spring, 1460': 29° 40' 48" N, 100° 00' 51" W; 0.5 mi. N Camp Wood. M.V.Z. 122672.

Mullen Hollow spring, 1940': 29° 57' 57" N, 99° 57' 52" W; 9.0 mi. NNE Barksdale (Edwards Co.). M.V.Z. 122673-122686.

Travis County

Barton Springs, 440': 30° 15' 51" N, 97° 46' 10" W; 1.9 mi. SW State Capitol, Austin. (*Eurycea* sp. nov.) T.N.H.X. T6317-T6321; T.T.U. uncatalogued (22 specimens); M.V.Z. 122712-122736; S.S.S. 13623-13633.

Stillhouse Hollow spring, 780': 30° 22' 20" N, 97° 45' 45" W; 6.9 mi. NNW State Capitol, Austin. M.V.Z. 122695-122703.

McDonald Well spring, 770': 30° 26' 57" N, 97° 51' 12" W; 3.1 mi. NNW Four Points (Hickmuntown). T.C.W.C. 44530-44532; CS-125 - CS-126; M.V.Z. 122705-122711.

Uvalde County

Onion Creek spring, 1500': 29° 34' 57" N, 99° 34' 51" W; 3.9 mi. SW Utopia. M.V.Z. 122764-122767.

Uvalde County concl.

Salt Marsh Creek spring, 1800': 29° 37' 03" N, 99° 36' 06" W; 4.2 mi. W Utopia. M.V.Z. 122727-122763.

Bludworth Ranch spring, 1500': 29° 31' 40" N, 99° 39' 12" W; 10.6 mi. SW Utopia. M.V.Z. 122768-122774.

Montell Creek spring, 1530': 29° 43' 28" N, 100° 04' 48" W; 5.2 mi. NW Montell. M.V.Z. 122775.

Val Verde County

San Felipe Springs, 910': 29° 22' 22" N, 100° 53' 09" W; 0.9 mi. ENE Del Rio. M.V.Z. 122791-122792.

Williamson County

San Gabriel River spring, 660': 30° 39' 15" N, 97° 40' 01" W1 1.3 mi. NNE Georgetown. M.V.Z. 122801.

Krienke Spring, 800': 30° 30' 22" N, 97° 44' 54" W; 3.2 mi. NW Round Rock. T.N.H.C. T1802-T1816; T6334-T6339; 31013 (42 specimens).

## Appendix II

This section provides existing data for a maximum of 46 populations of _Eurycea neotenes_ which were not possible to locate to the degree necessary for inclusion in Appendix I . A number of these appear to represent erroneous notations, and a certain number may be from sites listed in Appendix I .

Localities preceded by an asterisk are included on Figure 8 . Abbreviations of collections are listed in Appendix I , save for T.A.&I.C., Texas A&I University Collection, Kingsville.

### Bandera County

18 mi. NW Medina, Sutton Ranch. T.N.H.C. T2182-T2183.

23 mi. N Medina (probably 23 mi. NW Medina, as listed by Baker, 1961). T.N.H.C. T1886 (4 specimens).

7 mi. E Vanderpool, tributary of Mill Creek. T.N.H.C. 20807 (6 specimens).

Populations are reported from Bandera Creek, 6 mi. N Medina, and Middle Verde Creek, 8 mi. SW Bandera, by B.C. Brown, Baylor University (pers. com., 1970).

### Bell County

No additional localities.

### Bexar County

Helotes Creek, 5 mi. N Helotes. T.N.H.C. T6295-T6302; T.C.W.C. CS-151; K.U. 22229.

Culebra Creek, Helotes. F.M.N.H. 108596-108601.

Bexar County concl.

Helotes, creek on Melton's. T.N.H.C. 21671 (4 specimens).

Blanco County

1/4 and 3/4 mi. SE Blanco (Baker, 1961).

Waggoner's Cove spring, 4.0 mi. SE Blanco (F.S. Hendricks, pers. com., 1971).

Comal County

Voges Springs, Vogus (sic) Ranch, at KLRN radio transmitter. (pers. com., A. Hamilton, 1973).

Fishers Store, spring to NE. (pers. com., B.C. Brown, 1971).

Spring on Bear Creek, 4 mi. SW Sattler. T.T.U. uncatalogued (1 specimen).

Edwards County

4 mi. NW of Pulliam Creek, Barksdale. T.N.H.C. 20799 (19 specimens).

Gillespie County

*Fredericksburg. T.C.W.C. 14160-14163.

N Fredericksburg, Wolf Creek. T.C.W.C. 14118. (Note - Wolf Creek extends SW from Fredericksburg, and joins the Pedernales River SE of Fredericksburg; thus the indication "N" is probably in error).

Hays County

San Marcos Springs - this locality appears in a number of

<u>Hays County</u> concl.

ways, some of them erroneous. Aquarena Springs and Brown School are strict synonyms. Presumably inaccurate notations include: 1 mi. W San Marcos (T.C.W.C. 1512, 1514); 5 mi. E San Marcos (T.C.W.C. 4369); and San Marcos (numerous specimens).

Fern Bank Spring - this locality is widely reported as being 6.3 mi. NE Wimberley, following an error in the type description. Other presumably erroneous notations for this frequently visited site include: 6 mi. N Wimberley (T.C.W.C. 13275); 4 mi. SE Wimberley (T.C.W.C. 13701-13709; 14182, 14183); 4 mi. E Wimberley (T.C.W.C. 26827-26830); 3-4 mi. E Wimberley (T.C.W.C. 17575-17577).

1 mi. SE Fern Bank Springs. T.C.W.C. 26821-26824.

Wilson Creek, near Wimberley (A. Hamilton, pers. com., 1973).

Wimberley, along Blanco River 100 yards W highway 32 bridge (A. Hamilton, pers. com., 1973).

Spring near Twin Sister Mountain, 2 mi. from Wimberley (Uhlenhuth, 1921).

12 mi. WNW San Marcos on Skyline Ranch, Wimberley. T.N.H.C. 19290.

Rio Bonito Camp spring, on Blanco River (A. Hamilton, pers. com., 1973).

<u>Kendall County</u>

5 mi. N Boerne (Baker, 1961).

5 mi. WNW Boerne, W.M. Thornton Ranch (Baker, 1961).

*5.5 mi. WNW Boerne. T.N.H.C. 4824.

8 mi. W Boerne, Hall Ranch (Baker, 1961).

Several localities on Joshua Creek, near Welfare (B.C. Brown, pers. com., 1970).

<u>Kerr County</u>

6 mi. NNW Kerrville. T.N.H.C. T2314-T2316.

5 mi. W Kerrville, Turtle Creek (Baker, 1961). (Locality probably in error, as Turtle Creek is 7-12 mi. SW of Kerrville.)

8.3 mi. S, 2½ mi. W Kerrville, M.L. Pampell Ranch, tributary of Turtle Creek T.N.H.C. 11931 (Milstead, 1951).

13 mi. SW Kerrville, Chaney Ranch, 29° 54' 30" N, 99° 12' 30" W. T.A.&I.C. 1064 (63 specimens); 1308 (22 specimens); 1669 (117 specimens); 1822 (19 specimens); 2209 (27 specimens); 2480 (2 specimens); 3179 (108 specimens). Note - these collections combine specimens from Lambs Creek, Fall Creek, and the drainage of Verde Creek (A.H. Chaney, pers. com., 1973).

15 mi. SW Kerrville. K.U. 60769-60771.

<u>Medina County</u>

No additional localities reported.

Real County

10 mi. NE Leakey, Cypress Creek, spring. T.N.H.C. 21677 (36 specimens).

10 mi. NE Leakey, spring on East Frio River. T.N.H.C. 21675 (44 specimens).

15 mi. N Leakey, Moffit Ranch. T.C.W.C. 24452-24454.

15 mi. from Leakey. T.C.W.C. 23886.

Spring of Hours, Prade Ranch. F.M.N.H. 55097-55107; 55009; 55111-55122.

Travis County

*Spring near Marshall Ford Dam (Mansfield Dam) (Baker, 1961).

*Jack Dies Ranch, near Dodd City. T.N.H.C. 21640-21643.

Uvalde County

*Spring on bank of Frio River, about 2 mi. S of Garner State Park. T.C.W.C. 2114-2119; CS-166.

*Montell Springs, Montell. T.N.H.C. 21658-21659.

Montell Creek. T.N.H.C. 21672.

Val Verde County

No additional localities reported.

Williamson County

*1½ mi. NE Round Rock, Brushy Creek. T.N.H.C. 6242.

## Appendix III

This section provides locality data for 55 springs visited during the course of field work which were apparently not inhabited by *Eurycea neotenes*. The format is the same as in Appendix I.

### *Bandera County*

Kindla Spring, 1260': 29° 44' 54" N, 99° 06' 54" W.
Elm Creek spring, 1680': 29° 46' 06" N, 99° 17' 18" W.
North Prong Medina River spring, 1650': 29° 51' 25" N, 99° 21' 45" W.

### *Bell County*

Salado Springs, 560': 30° 56' 23" N, 97° 32' 06" W.

### *Bexar County*

San Antonio Springs, 680': 29° 27' 56" N, 98° 28' 06" W.

### *Blanco County*

290x281 spring, 1280': 30° 12' 32" N, 98° 22' 28" W.
Crabapple Creek spring, 1380': 30° 06' 08" N, 98° 30' 35" W.

### *Comal County*

Frio Spring, 1100': 29° 55' 55" N, 98° 10' 46" W.
Lonesome Valley Spring, 1060': 29° 56' 00" N, 98° 10' 21" W.

## Kendall County

Simmons Creek spring, 1080': 29° 54' 53" N, 98° 29' 57" W.

Little Water Cave creek spring, 1100': 29° 53' 16" N, 98° 31' 10" W.

Alzafar creek spring, 1280': 29° 53' 00" N, 98° 39' 19" W.

Swede Creek spring, 1180': 29° 52' 02" N, 98° 34' 38" W.

Panther Creek spring, 1100': 29° 52' 18" N, 98° 32' 42" W.

Fourlevel Water Cave spring, 1808': 29° 52' 41" N, 98° 31' 33" W.

## Kerr County

Hasenwinkle Creek spring, 1800': 30° 04' 14" N, 98° 57' 40" W.

Cross Creek Ranch spring, 1850': 30° 06' 57" N, 98° 57' 40" W.

East Town Creek spring, 1820': 30° 05' 58" N, 99° 07' 31" W.

Lange Box Spring, 2000': 30° 02' 05" N, 99° 23' 45" W.

Guadalupe headwaters spring, 1920': 30° 03' 10" N, 99° 29' 42" W.

Bee Caves Creek lower spring, 1900': 30° 03' 30" N, 99° 27' 33" W.

Bee Caves Creek upper spring, 1940': 30° 02' 13" N, 99° 25' 21" W.

Johnson Creek spring, 1900': 30° 10' 46" N, 99° 22' 45" W.

Honey Creek Ranch spring, 1900': 30° 06' 12" N, 99° 22' 07" W.

## Edwards County

Pulliam Creek lower spring, 1800': 29° 50' 22" N, 100° 07' 19" W.

Pulliam Creek upper spring, 1820': 29° 51' 02" N, 100° 07' 45" W.

## Gillespie County

Spring Creek spring, 2010': 30° 20' 35" N, 99° 04' 48" W.

Live Oak Creek spring, 2020': 30° 21' 08" N, 99° 01' 26" W.

Pecan Creek spring, 2000': 30° 22' 03" N, 98° 58' 22" W.

Willow Creek spring, 1900': 30° 21' 51" N, 98° 45' 48" W.

## Hays County

Smith Creek lower spring, 1080': 30° 01' 02" N, 98° 04' 27" W.

Smith Creek upper spring, 1100': 30° 01' 35" N, 98° 04' 45" W.

Ben McCulloch Spring, 940': 30° 07' 40" N, 98° 00' 45" W.

Blanco River spring, 820': 29° 59' 32" N, 98° 05' 30" W.

spring 1.5 mi E Payton, 1270': 30° 06' 33" N, 98° 16' 08" W.

Rancho Cima Dam spring, 1040': 29° 56' 23" N, 98° 09' 06" W.

spring 1 mi SE Signal Hill, 880': 30° 10' 48" N, 97° 56' 07" W.

### Kinney County

Las Moras Springs, 1100': 29° 18' 32" N, 100° 25' 16" W.

### Real County

Deer Creek spring, 1620': 29° 39' 27" N, 99° 40' 03" W.

Eagle Cliff spring, 1880': 29° 57' 38" N, 99° 57' 12" W.

### Travis County

Sheep Hollow spring, 980': 30° 35' 08" N, 97° 58' 07" W.

Spicewood Springs, 730': 30° 21' 55" N, 97° 44' 59" W.

Canyon Spring, 1020': 30° 15' 35" N, 97° 53' 03" W.

Short Spring Branch spring, 850': 30° 15' 00" N, 97° 53' 18" W.

### Uvalde County

Bear Creek lower spring, 1700': 29° 36' 18" N, 99° 36' 50" W.

Bear Creek upper spring, 1740': 29° 36' 39" N, 99° 36' 30" W.

Cowan Springs, 1260': 29° 30' 17" N, 99° 42' 27" W.

Cold Springs Ranch Spring, 1410': 29° 36' 45" N, 99° 44' 25" W.

Concan Springs, 1220': 29° 29' 47" N, 99° 42' 40" W.

### Williamson County

Andice spring, 970': 30° 46' 58" N, 97° 50' 16" W.

Sycamore Springs, 990': 30° 48' 48" N, 97° 55' 33" W.

S Fork San Gabriel spring, 850': 30° 37' 06" N, 97° 50' 40" W.

Williamson County concl.

Jim Hagg Road spring, 830': 30° 40' 31" N, 97° 45' 38" W.

Crockett Gardens Springs, 810': 30° 39' 50" N, 97° 45' 05" W.

Sideriver spring, 760': 30° 36' 00" N, 97° 45' 00" W.

# Appendix IV

This section provides locality data for the 29 known or reported troglobitic populations of the Texas *Eurycea*, and lists specimen numbers and repositories of the available material. The form of citation employed in Appendix I is retained here, with the modification that locality data refer to the cave entrance rather than the point(s) in the cave inhabited by salamanders. Additional abbreviations: D.B.W., David B. Wake, Museum of Vertebrate Zoology; and U.S.N.M., United States National Museum of Natural History.

## Bandera County

Sutherland Hollow Cave, 1800': 29° 45' 02" N, 99° 25' 18" W; 10.9 mi. SW Medina. No specimens.

Haby Water Cave, 2270': 29° 51' 45" N, 99° 33' 38" W; 7.8 mi. NNE Vanderpool. M.V.Z. 119936; T.T.U. uncatalogued (1 specimen).

## Bexar County

Elm Springs Cave, 965': 29° 35' 00" N, 98° 34' 00" W; 0.8 mi SSE junction of highways 1604 and 1535, San Antonio. S.S.S. 13640-13643; T.C.W.C. 38237; 44494; CS-159; CS-160.

## Blanco County

T Cave, 1180': 30° 04' 36" N, 98° 19' 46" W; 0.75 mi SSW junction of Boardhouse Creek and Blanco River, 6.0 mi. E Blanco. No specimens.

## Comal County

Fischer's Well, 1140': 29° 58' 53" N, 98° 15' 36" W; in settlement of Fischer. T.T.V. uncatalogued (1 specimen).

Plumly Ranch Cave, 1100': 29° 54' 23" N, 98° 26' 39" W; 3.1 mi. NW Spring Branch. No specimens.

Bender's Cave, 1100': 29° 53' 55" N, 98° 26' 42" W; 2.8 mi. NW Spring Branch. M.V.Z. 120466-120530; 122814; T.T.U. uncatalogued (5 specimens).

Honey Creek Cave, 1100': 29° 50' 51" N, 98° 29' 30" W; 5.8 mi. SW Spring Branch. *E neotenes*: M.V.Z. 120382-120383; 120385-120388; intermediate morph: M.V.Z. 120384; 120389-120391; *E*. *tridentifera*: M.V.Z. 120531-120560; T.N.H.C. 31521-31534 (paratypes); T.C.W.C. 44484-44486; CS-162; T.T.U. uncatalogued (10 specimens); U.S.N.M. 153780 (holotype); 153781-153785 (paratypes); D.B.W. 421-423.

Kappelman Salamander Cave, 1035': 29° 45' 46" N, 98° 23' 08" W; 3.0 mi. SE junction highways 46 and 281, 16 mi. WNW New Braunfels. S.S.S. 13505-13507; T.T.U. uncatalogued (2 specimens).

Calmbach Cave, 1180': 2.2 02.4 mi. NW Bulverde. T.T.U. uncatalogued (1 specimen).

Grosser's Sinkhole, 1270': 29° 44' 52" N, 98° 36' 48" W; 6.0 mi. SSW Bergheim. M.V.Z. 120583-120597; T.T.U. uncatalogued (4 specimens) T.C.W.C. 44487-44488; CS-158.

Comal County concl.

Badweather Pit, 1280': 29° 45' 21" N, 98° 37' 13" W; 5.5 mi. SW Bergheim. M.V.Z. 120561-120582; T.T.U. uncatalogued (20 specimens); T.C.W.C. 44489-44492; CS-161.

Kendall County

Kneedeep Water Cave, 1100': 5.2-6.5 mi. W Spring Branch, N bank Guadalupe River. No specimens.

Little Water Cave, 1100': 29° 53' 18" N, 98° 31' 11" W; 5.4 mi. NE Bergheim. No specimens.

Deadman's Cave, 1140': 29° 53' 10" N, 98° 37' 01" W; 10.0 mi. NE Boerne. M.V.Z. 121377-121391.

Alzafar Water Cave, 1260': 29° 53' 05" N, 98° 39' 19" W; 8.3 mi. NE Boerne. M.V.Z. 121368-121375; T.C.W.C. 44502-44503; 45354; CS-155 - CS-157.

Golden Fawn Cave, 1260': 29° 53' 00" N, 98° 40' 10" W; 7.4 mi. NNE Boerne. M.V.Z. 121376.

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

Behr's Cave, 1340': 29° 55' 51" N, 98° 42' 20" W; 10.3 mi. N Boerne. M.V.Z. 121392-121395.

Cascade Caverns, 1320': 29° 45' 48" N, 98° 40' 42" W; 3.3 mi. SE Boerne. U.S.N.M. 123594 (holotype); T.C.W.C. 1195-1197; T.N.H.C. 4822, 6326, 6331-6333; C.U. 4551; F.M.N.H. 91040, 91041, 91043, 91054; M.V.Z. 68381, 68382; T.T.U. uncatalogued (2 specimens).

Kendall County concl.

Cascade Sinkhole, 1320': $29^\circ$ 45' 49" N, $98^\circ$ 40' 53" W; 3.2 mi. SE Boerne. S.S.S. 13634-13639; T.T.U. uncatalogued (2 specimens).

Schwarz Cave, 1340': $29^\circ$ 44' 40" N, $98^\circ$ 40' 37" W; 4.5 mi. SE Boerne. No specimens.

Medina County

Valdina Farms Sinkhole, 1210': $29^\circ$ 30' 58" N, $99^\circ$ 23' 58" W; 15.2 mi. NNW D'Hanis. T.N.H.C. 21791 (holotype); 21786-21790, 21792-21805 (paratypes); M.V.Z. 122130-122141; D.B.W. 424, 828; T.T.U. uncatalogued (7 specimens); T.C.W.C. 38233, 38235, CS-168.

Real County

Tucker Hollow Cave, 1880': $29^\circ$ 44' 33" N, $99^\circ$ 46' 42" W; 1.6 mi. NW Leakey. M.V.Z. 122687-122694; T.T.U. uncatalogued (2 specimens).

Travis County

Barton Springs, 440': $30^\circ$ 15' 51" N, $97^\circ$ 46' 10" W; 1.9 mi. SW Capitol, Austin. T.N.H.C. 6317-6321; M.V.Z. 122712-122726; S.S.S. 13623-13633, 15006-15031; T.T.U. uncatalogued (22 specimens).

Salamander Cave, 800': $30^\circ$ 22' 03" N, $97^\circ$ 45' 14" W; 6.5 mi. NNW Capitol, Austin. T.T.U. uncatalogued (8 specimens).

Uvalde County

Cave near Concan: probably Bludworth Ranch, 4-6 mi. NE Concan. No specimens.

Carson Cave, 1480': 29° 28' 50" N, 100° 04' 44" W. 5.1 mi. SW Montell. M.V.Z. 122776-122790.

Val Verde County

Fourmile Cave, 1070': 29° 25' 33" N, 100° 53' 23" W; 3.6 mi. N Del Ril. T.N.H.C. 21678 (4 specimens, now missing); M.V.Z. 122793-122800; T.T.U. uncatalogued (1 specimen).

Comstock Crack, 1400': 29° 41' 25" N, 101° 11' 28" W; 1.0 mi. WNW Comstock. No specimens.

# Appendix V

Localities and respositories of cleared and stained specimens of Eurycea pterophila, E. nana, and E. neotenes examined in Chapter VII. General localities are followed by coordinates of latitude and longitude. Abbreviations: M.V.Z.: Museum of Vertebrate Zoology, University of California, Berkeley; T.C.W.C.: Texas Cooperative Wildlife Collection, Texas A and M University; T.N.H.C.: Texas Natural History Collection, University of Texas, Austin; T.T.U.: uncatalogued material, Dr. R. W. Mitchell, Texas Tech University.

Eurycea pterophila (33 specimens), Hays County, Fern Bank Spring (29° 59' 00" N, 98° 00' 45" W): M.V.Z. 120923-120938; M.V.Z.-DBW 231-233. T.C.W.C. CS-120 - CS-124; CS-131 - CS-134. T.N.H.C. 31004 (five specimens).

Eurycea nana (40 specimens),Hays County, San Marcos Spring (29° 53' 38" N, 97° 55' 47" W): M.V.Z. 121042-121067. T.C.W.C. CS-135 - CS-148.

Eurycea neotenes (59 specimens), Bandera County, Mill Creek (29° 47' 30" N, 99° 30' 10" W): M.V.Z. 119937-119952. Bexar County, 5 miles (=8 km) N Helotes (29° 38' 15" N, 98° 41' 40" W): M.V.Z. 120027-120034, 120069. T.C.W.C. CS-151. Comal County, Bender's Cave (29° 53' 55" N, 98° 26' 42" W): M.V.Z. 120487-120492. Gillespie County, Henderson Branch (30° 08' 11" N, 99° 14' 18" W): T.C.W.C. CS-113 - CS-119, CS-127 - CS-130. Kendall

County, Alzafar Water Cave (29° 53' 05" N, 98° 39' 19" W): T.C.W.C. CS-155 - CS-157. Kerr County, Fessenden Branch (30° 09' 58" N, 99° 21' 03" W): M.V.Z. 121480-121483; Lambs Creek (29° 55' 20" N, 99° 14' 21" W): M.V.Z. 121929-121931. Real County, Cypress Creek (29° 47' 46" N, 99° 38' 58" W): T.C.W.C. CS-149, CS-150; East Frio River (29° 47' 46" N, 99° 40' 02" W): M.V.Z. 122541; 15 miles (=24 km) N Leakey: T.C.W.C. CS-167. Travis County, Salamander Cave (30° 22' 03" N, 97° 45' 14" W): T.T.U. SC-1 - SC-3.