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Secondary Contact and Hybridization in the Texas Cave Salamanders *Eurycea neotenes* and *E. tridentifera*

SAMUEL S. SWEET

Unusual levels of individual and populational variation and character discordance in three samples of troglobitic *Eurycea* from the Edwards Plateau of central Texas indicate hybridization between *Eurycea neotenes* and *E. tridentifera*. The two species are microsympatric but exhibit habitat segregation in one case, are contiguously allopatric in the same cave system in another, and appear to interact as vagrants in the third. *E. neotenes* and *E. tridentifera* seem to be evolving reproductive isolation at Honey Creek Cave, where hybrids are uncommon. *Eurycea troglodytes* and *E. latitans* are shown to be invalid taxa, the former consisting of a hybrid swarm of temporally variable composition and the latter being a troglobitic population of *E. neotenes* which episodically incorporates individuals of *E. tridentifera*. Variation in the interactions of the parental species on contact is ascribed to differences in the opportunity for ecological segregation permitted, the relative frequencies of incursion of the parental taxa through time, and differences in the escape behavior of intermediate and advanced troglobites in cave systems which periodically receive influxes of flood-borne epigeal fish.

DISTRIBUTIONAL patterns consisting of arrays of allopatric, distinctive populations pose a suite of familiar systematic problems, whether these patterns are interpreted to have originated through dispersal or vicariance. Such populations are likely to have been genetically "small" at one or more points in their histories, and frequently occur under circumstances favoring strong and often similar selective regimes as a consequence of their restriction to favorable islands of habitat. Wiley (1981) has recognized the inability of cladistic methodologies to resolve relationships within groups of peripheral isolates or among relict populations, where most character changes may be autapomorphic; the situation may be even less amenable to either cladistic or phenetic approaches owing to parallel responses to selection among the isolated units.

All of the above features characterize troglobitic taxa, which have the additional problem that actual distributions are difficult to fully disclose. The usual course of action has been to name as many taxa as can be diagnosed on morphological criteria, with the result that the evolutionary histories advanced seem unduly complex in relation to outgroup reference points. Under these circumstances rare events of sympatry assume special importance by providing a within-group metric for the magnitude of evolutionary divergence.

Populations of the small, paedomorphic sal-

amanders of the plethodontid genus *Eurycea* inhabiting the limestone plateau of central Texas constitute a specimen case of parallel evolution in distributional relicts (Sweet, 1978). Prominent in this group is a graded series of cave-adapted populations ranging from those of unmodified epigeal (surface-dwelling) morphology to advanced troglobites characterized by depigmentation, extreme eye reduction and hypertrophy of locomotor and trophic structures (Mitchell and Reddell, 1965; Mitchell and Smith, 1972). High levels of concordance among character states exist in interpopulational comparisons, and apart from ontogenetic allometry intrapopulational variability is characteristically low. Geographic and geologic considerations indicate that many phenotypically similar populations are independently derived and have evolved in a parallel fashion in concert with local geomorphic events (Sweet, 1978, provides details). One is thus left with the prospect of recognizing polyphyletic taxa or diagnosing numerous cryptic forms unless it is possible to show that morphological differentiation correlates poorly with the acquisition of reproductive isolation.

In the course of examining differentiation in these salamanders I found that specimens from three of 22 troglobitic populations were atypical in displaying high levels of individual variation and character discordance. In one case three discrete phenotypes are present: individuals re-

ferable to the widely-distributed epigeic species *Eurycea neotenes*; individuals referable to the advanced troglobite *E. tridentifera*; and specimens of variable and discordant intermediacy. Two other atypical populations largely consist of individuals in this third category, and represent the currently recognized species *Eurycea latitans* and *E. troglodytes*. By comparison with the first case I will argue that these taxa are of hybrid origin and thus invalid, and employ this interpretation to help define the scale of evolutionary divergence applicable to troglobitic populations of the Texas *Eurycea*.

MATERIALS AND METHODS

Primary data in this paper derive from samples of salamanders from three geographically restricted regions of the southeastern Edwards Plateau, in each case the type locality of the indicated troglobitic species. Precise localities and museum numbers for this material are available elsewhere (Sweet, 1978); general localities are illustrated in Fig. 1. Sites and samples are as follows: Honey Creek Cave, Comal Co. (60 *E. tridentifera*, 6 *E. neotenes* and 4 intermediate individuals); Valdina Farms Sinkhole, Medina Co. (39 *E. troglodytes*); and the Cascade Caverns system, Kendall Co. (22 *E. latitans*). Also included are 32 specimens of an undescribed troglobitic *Eurycea* from Travis Co. Because phenotypically pure *E. neotenes* and *E. tridentifera* are rare or absent in Valdina Farms Sinkhole and the Cascade Caverns system, I employed reference series of these species from the nearest localities for comparison with the *E. troglodytes* and *E. latitans* samples. For *E. troglodytes*, reference samples were 53 *E. neotenes* from nearby Seco Creek, Bandera Co., and 47 *E. tridentifera* from Badweather Pit in southwestern Comal Co. The latter sample and 50 *E. neotenes* from the headwaters of Cibolo Creek, Kendall Co. served as reference samples for the analysis of *E. latitans*. Seco Creek *E. neotenes* and Badweather Pit *E. tridentifera* were used in comparisons involving *E. sp.*

The following measurements and counts were employed: standard length (SL)—tip of snout to posterior margin of cloaca; axilla-groin length (AG)—posterior margin of forelimb to anterior margin of hind limb; hind limb length (HLL)—groin to tip of third digit; head length *a* (HLA)—tip of snout to gular fold at midventral line; head length *b* (HLB)—tip of snout to dorsal margin of third gill ramus; head length *c*

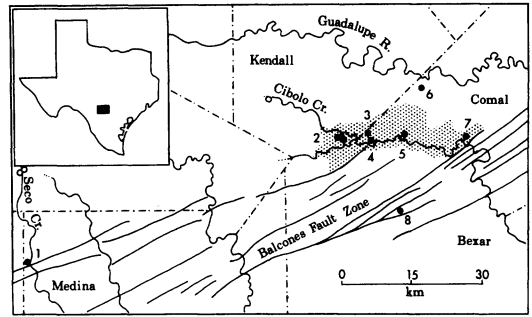


Fig. 1. Map of the southeastern margin of the Edwards Plateau, illustrating the distribution of several troglobitic populations of *Eurycea* with respect to the Balcones Fault Zone and the Cibolo sinkhole plain (stippled area). Numbered localities are as follows: 1, Valdina Farms Sinkhole (*E. troglodytes*);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

(HLC)—posterior margin of eye to base of third gill ramus; head width (HW)—span at jaw articulation; eye diameter (ED)—silhouette of optic cup in transverse plane; interorbital distance (IOD)—span between optic cups; number of trunk vertebrae (TV)—atlas and sacrum excluded; premaxillary (PM), vomerine (VO), palatopterygoid (PT) and dentary (D) teeth—numbers of tooth pedicels on each element, rather than number of seated teeth, left and right sides combined. All measurements were made to 0.1 mm with dial calipers (SL) or an ocular micrometer; vertebral and tooth counts were taken either from cleared and stained specimens or high-resolution radiographic negatives.

Data were analyzed on the U.C. Berkeley CDC 6400 computer (SPSS correlation and discriminant analyses); values of Kendall's Coefficient of Concordance were calculated manually. Specimens with incomplete data were excluded; sample sizes vary accordingly and are specified for each series of tests.

RESULTS

Characteristics of sites and populations.—Honey Creek Cave is one of a number of small stream

caves opening into the shallow canyon of the middle portion of the Guadalupe River in Kendall and western Comal counties (Fig. 1). Most of these caves are rather short (<1 km) and drain fissures and sinkholes of the adjacent Guadalupe terrace; Honey Creek Cave is much longer (>11 km), and is known to extend beneath the surface divide into the Cibolo sinkhole plain to the south (Anon., 1983). While most of the Guadalupe caves have populations of *E. neotenes*, Honey Creek Cave is the only one known to contain a population of *E. tridentifera* as well; this species is widespread in the caves of the Cibolo sinkhole plain (Sweet, 1977a). The two species show habitat segregation in sympatry, *E. neotenes* occupying the outflow and cave mouth with marginal overlap into the deep cave zone occupied by *E. tridentifera*. The four intermediate individuals were collected in the first 10 m of the cave.

E. tridentifera is a depigmented, highly derived troglobite with a large head, short trunk and thin, elongate limbs; the eyes are much reduced and typically lack lenses. The sympatric *E. neotenes* population is of typical epigeal morphology, being heavily pigmented with a long trunk, short limbs and eyes of normal size and structure. I interpret the four remaining individuals as *E. neotenes* × *tridentifera* hybrids, as supported below. Fig. 2A illustrates representative specimens from this locality.

Valdina Farms Sinkhole is a large collapse sink intersecting a horizontal stream passage with no local outlet; this passage lies 30–60 m below minimum land surface in the region, and is presumably a tributary of the main aquifer of the Balcones Fault Zone (Fig. 1). The accessible passages of Valdina Farms Sinkhole are adjacent and parallel to the Woodward Fault, a major structure having surface exposure of about 60 km and trending northeast towards the known range of *E. tridentifera*.

Eurycea troglodytes was described on the basis of 20 specimens (Baker, 1957); since that time an additional 25 have been secured, mostly in 1967 (7) and 1972–4 (14). This population differs strikingly from others of the Texas *Eurycea* in displaying considerable individual variation in pigmentation and morphology, as was noted by Baker (1957) and figured by Bogart (1967: pl. 6B). A series of *E. troglodytes* from the 1974 collection is illustrated in Fig. 2C; extreme individuals in this sample are superficially similar to *E. neotenes* or *E. tridentifera* (compare Figs.

2A, C). Evidence is presented below that *E. troglodytes* is a hybrid swarm.

The Cascade Caverns system is comprised of several sinkholes on the western edge of the Cibolo sinkhole plain (Fig. 1). This region displays the most mature karst topography of the Edwards Plateau (Smith, 1971); stream passages are developed on two or more levels, and are presumably integrated into major trunk channels below since the system behaves as a unit during floods. As is the case at Valdina Farms Sinkhole, discharge occurs into the adjacent subterranean channels of the Balcones Fault Zone.

Eurycea latitans is now known from three adjacent sinkhole systems: Cascade Caverns, Cascade Sinkhole and Pfeiffer Water Cave. The species was described (Smith and Potter, 1946) from a series of 20 specimens, only two of which are extant; a few other specimens were collected as early as 1933. I have located 13 specimens taken prior to 1950 (several in poor condition), and 10 specimens collected since 1965. The material from early collections appears to differ from recent specimens in being paler and stouter (Fig. 2B); the latter are not easily distinguished from populations inhabiting several of the Guadalupe caves, which I have considered to represent *E. neotenes* (Sweet, 1978). Populations of *E. tridentifera* occupy caves in the Cibolo plain only 5.5–6.0 km to the east of the Cascade system (Fig. 1) and are thought to have physical access to it.

Individual variation in populations.—Most of the characters showing directionality in the epigeal-troglobitic trend are cumbersome as indices of the degree of troglobitic specialization of a population: they are either difficult to quantify (pigmentation, eye structure) or exhibit moderate to strong ontogenetic allometry (proportions and tooth counts). The number of trunk vertebrae is easily determined and directional, and may serve as an index of specialization as well as being a simple indicator of unusual levels of intrapopulational variability. Distributions of trunk vertebral counts in several population samples of epigeal and troglobitic *Eurycea* are presented in Table 1. Strong directional change is evident, all populations of *E. tridentifera* being strongly modal for 14 trunk vertebrae, whereas nearly all epigeal and cave populations here referred to *E. neotenes* have modes of 17. No population with a mode of 15 is known; modes

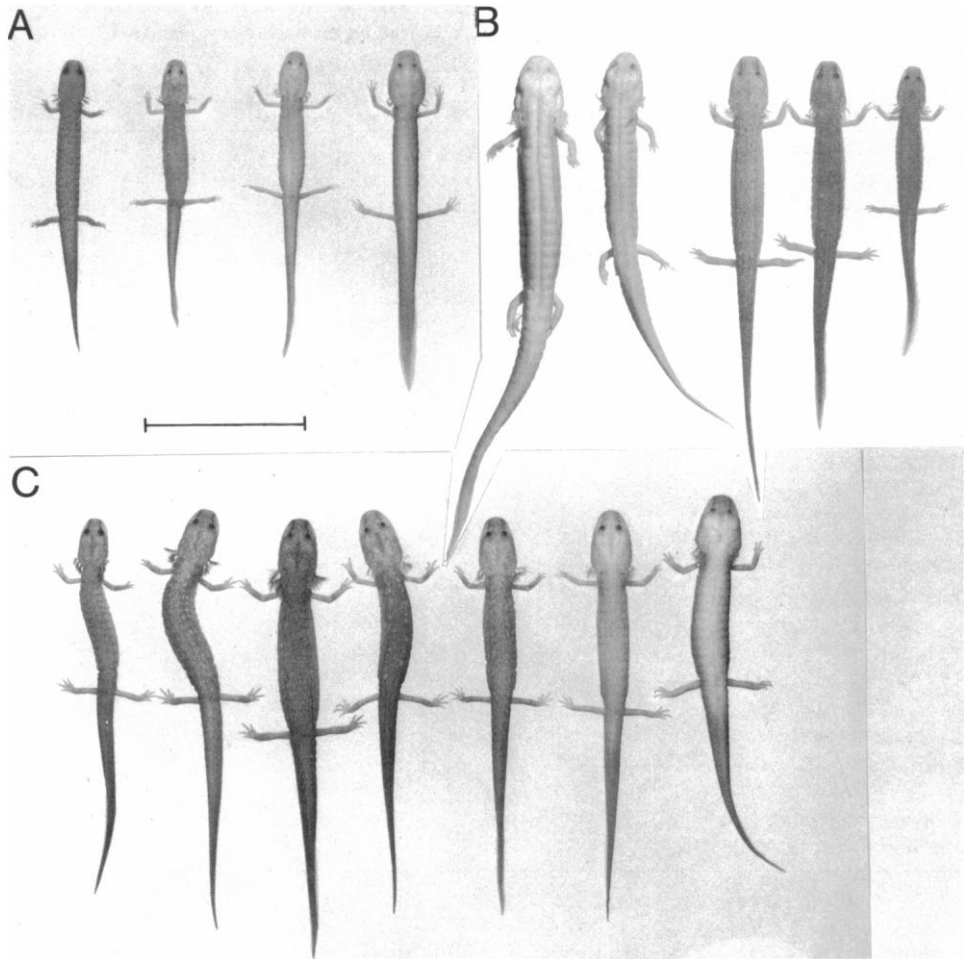


Fig. 2. Representative *Eurycea* from populations discussed in the text: A) Honey Creek Cave, Comal County; from l-r, *Eurycea neotenes* (MVZ 120383), two presumed hybrids (MVZ 120390-91) and *E. tridentifera* (MVZ 120544); B) Cascade Caverns system, Kendall County; *Eurycea latitans* (left pair, SSS 25655-56, Gen. Biol. Supply House, Chicago, Ill., collected "prior to 8/37"; others, SSS 13636-38, collected in January, 1976); and C) Valdina Farms Sinkhole, Medina County; *Eurycea troglodytes* (MVZ 122135-41, r-l) from the 1974 collection, showing range of phenotypes present in this population. Scale bar = 30 mm.

of 16 characterize four samples of salamanders which are otherwise structurally intermediate. Of these, only the undescribed species displays a strong mode; *E. troglodytes*, *E. latitans* and the Honey Creek Cave intermediates show considerable individual variation in this character, each having standard deviations >0.80 compared to a range of 0.0-0.46 in the 15 remaining samples. The Honey Creek Cave sample is clearly divisible into three morphs (*E. tridentifera*, *E. neotenes* and intermediates) on the basis of ex-

ternal appearance; if not so partitioned this "population" has a standard deviation of 1.06 vertebrae. These values are considerably in excess of any found in a survey of vertebral numbers in 119 additional spring and cave populations of the Texas *Eurycea* (Sweet, 1978), and are consistent with the view that these samples are of hybrid origin.

The level of individual variation in allometric characters (proportions and tooth counts) may be partially assessed by examination of corre-

TABLE 1. DISTRIBUTIONS AND STANDARD DEVIATIONS OF NUMBER OF TRUNK VERTEBRAE IN 18 SAMPLES OF TEXAS *Eurycea*. Populations of *E. neotenes* are arranged in east to west sequence.

Species Population	Number of trunk vertebrae						SD
	13	14	15	16	17	18	
<i>E. neotenes</i>							
Krienke Spring				9	32	1	0.455
Puter Creek				7	89	9	0.378
Honey Creek Cave					6		0.000
Cibolo Creek					96	13	0.336
Fall Creek				5	206	12	0.188
Seco Creek				4	42	7	0.456
Mill Creek				9	163	2	0.247
Ash Hollow				10	216	15	0.329
Dutch Creek				5	120	4	0.265
<i>E. neotenes</i> × <i>tridentifera</i>							
Honey Creek Cave			1	2	1		0.816
<i>E. latitans</i>							
Cascade Caverns system			5	8	6	1	0.847
<i>E. troglodytes</i>							
Valdina Farms Sinkhole		1	4	20	14	1	0.808
<i>E. sp.</i>							
Travis County			2	35	3		0.357
<i>E. tridentifera</i>							
Honey Creek Cave	9	48	3				0.273
Badweather Pit	3	43	1				0.292
Grosser's Sinkhole	2	14	5				0.301
Kappelman Salamander Cave		5					0.000
Elm Springs Cave	1	7					0.354

lation coefficients between pairs of variables such as those listed in Table 2. While the degree of correlation in body proportions is generally high in all populations examined, the more specialized troglobites show reduced correlations of eye size and tooth counts with body size. This decrease is principally due to a doubling of tooth numbers in advanced troglobites (with a lesser component of a slight increase in variance), and to a decoupling of eye and body growth rates in *E. tridentifera*. The eyes of this species cease growth soon after hatching, in this respect resembling *Typhlomolge rathbuni* rather than other troglobitic *Eurycea*.

The three samples characterized by high vertebral variation do not stand out as strongly in the data of Table 2; the small size of the sample of intermediate specimens from Honey Creek Cave precludes meaningful interpretation, and values for *E. latitans* fall within the range observed in troglobitic populations of *E. neotenes*.

Only the *E. troglodytes* sample displays correlations which are generally lower than any of the corresponding values for *E. neotenes* or *E. tridentifera*. These results are perhaps to be expected in any situation where ontogenetic allometry is relatively strong, for an overall correlation with size can conceal considerable individual variation as emphasized in the discussion of character concordance below.

A somewhat different and more powerful approach to the characterization of individual variability can be derived from discriminant analysis. Discriminant analysis seeks to maximize the effects of differences present in a character matrix representing two or more specified groups, producing character weightings which define the locations of individuals in discriminant space through one or more linear functions. The discriminating power of the technique can easily exceed the validity of its biological interpretation, and discrimination of

TABLE 2. CORRELATION COEFFICIENTS OF BODY PROPORTIONS AND NUMBERS OF TEETH IN 19 SAMPLES OF TEXAS *Eurycea*. Average correlation coefficients were calculated through transformation to Z. Values marked with a † are not significant at the 0.05 level. Symbols in Materials and Methods.

Species Population	N	$\frac{HW}{SL}$	$\frac{HLL}{SL}$	$\frac{ED}{HW}$	$\frac{PM}{HW}$	$\frac{VO}{HW}$	$\frac{DT}{HW}$	r
<i>E. neotenes</i>								
Honey Creek Cave	6	0.90	0.94	0.76	0.78	0.58†	0.78	0.83
Cibolo Creek	50	0.98	0.98	0.93	0.87	0.85	0.93	0.94
Seco Creek	31	0.96	0.96	0.89	0.53	0.60	0.56	0.84
Salamander Cave	8	0.90	0.63	0.82	0.40†	0.62	0.62	0.70
Bender's Cave	38	0.96	0.96	0.75	0.77	0.76	0.75	0.87
Deadman's Cave	15	0.99	0.98	0.95	0.91	0.95	0.92	0.96
Alzafar Water Cave	14	0.99	0.91	0.85	0.86	0.86	0.85	0.91
Tucker Hollow Cave	9	0.99	0.98	0.98	0.95	0.83	0.84	0.97
Carson Cave	15	0.98	0.97	0.81	0.88	0.83	0.88	0.92
Fourmile Cave	8	0.97	0.94	0.82	0.66	0.27†	0.59†	0.81
<i>E. neotenes</i> × <i>tridentifera</i>								
Honey Creek Cave	4	0.88†	0.39†	0.51†	0.68†	0.91	0.85†	0.76†
<i>E. latitans</i>								
Cascade Caverns system	17	0.96	0.95	0.80	0.61	0.60	0.84	0.85
<i>E. troglodytes</i>								
Valdina Farms Sinkhole	38	0.85	0.72	0.42	0.20†	0.24†	0.28†	0.51
<i>E. sp.</i>								
Travis County	34	0.93	0.91	0.68	0.61	0.73	0.56	0.78
<i>E. tridentifera</i>								
Honey Creek Cave	38	0.91	0.85	0.31	0.45	0.52	0.51	0.66
Badweather Pit	37	0.95	0.91	0.02†	0.75	0.61	0.60	0.74
Grosser's Sinkhole	17	0.86	0.86	0.10†	0.14†	0.36†	0.83	0.63
Kappelman Salamander Cave	4	0.98	0.90	0.84†	0.56†	0.76†	0.51†	0.84
Elm Springs Cave	8	0.88	0.86	0.01†	0.49†	0.92	0.89	0.78

samples per se must be interpreted with especial caution. Successful allocation of specimens to the "right" groups should be no surprise—this is what the method is designed to do—; however, misallocations are of greater interest and constitute very strong evidence for phenotypic similarity. In essence I have employed the failure of the a posteriori classification option of the discriminant program as a clustering technique. This is most powerful when each specimen is initially assigned to one of the three groups (intermediate, *E. neotenes* or *E. tridentifera*), for intermediate individuals which are misclassified may actually be members of a parental taxon within the putative hybrid population. The relative position of specified groups in discriminant space is also of interest in analyses which encompass the range of an adaptive trend such as the series of troglotic populations considered here.

Discriminant analyses were performed with trios of population samples consisting of *E. neotenes*, *E. tridentifera* and each of the four structurally intermediate samples (Honey Creek Cave, *E. latitans*, *E. troglodytes* and *E. sp.*). *E. neotenes* and *E. tridentifera* are the probable parental taxa if a situation of hybridization exists; however, these species are known to occur sympatrically only at Honey Creek Cave. In these tests prior probabilities were set equal, and all variables were entered concurrently. Characters employed and standardized character weightings are listed in Table 3.

The first function explains 94, 77, 98 and 96% of the total variance in the Honey Creek Cave, Valdina Farms Sinkhole, Cascade system and *E. sp.* populations and their respective reference groups, with heavy loadings for trunk vertebrae, standard length and hind limb length, in order of decreasing influence. The second

TABLE 3. 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		<i>E. troglodytes</i>		<i>E. latitans</i>		<i>E. sp.</i>	
	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

function encompasses the remaining variance (by definition), with loadings distributed throughout the character set in no apparent pattern (Table 3).

Scatter plots of individual scores on the two discriminant axes are presented in Fig. 3. These plots display the relative position and degree of

dispersion of groups; in terms of spread on the first axis the *E. tridentifera*, *E. neotenes* and *E. sp.* samples are less variable than are the samples of *E. troglodytes*, *E. latitans* and the Honey Creek Cave intermediates to which they are compared.

By designating each population (two refer-

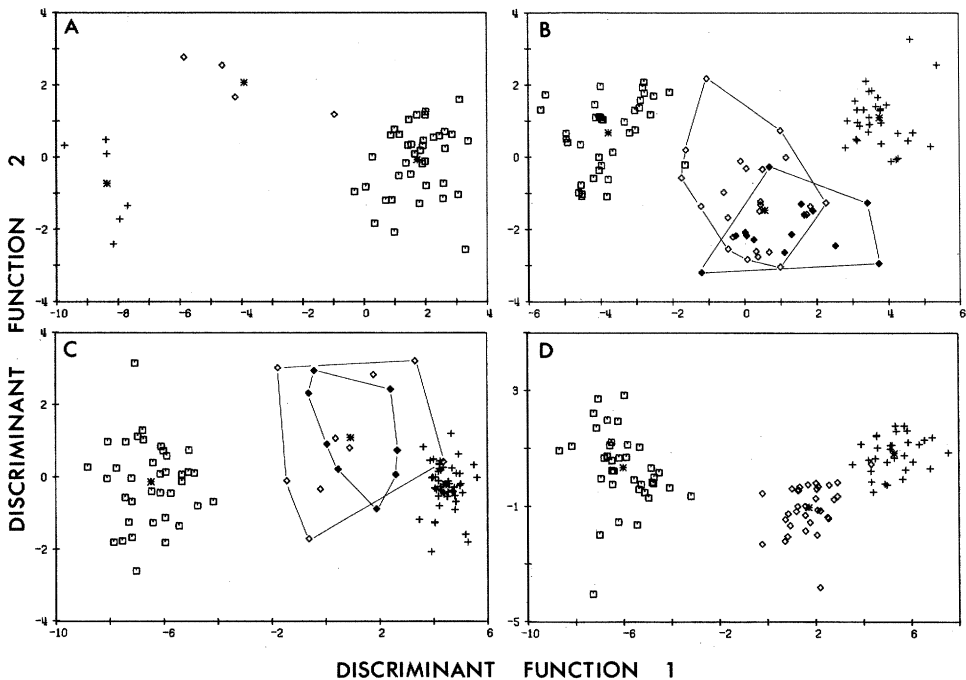


Fig. 3. Scatter plots of discriminant scores for structurally intermediate specimens (diamonds), and *Eurycea neotenes* (crosses) and *E. tridentifera* (squares) reference groups (see text for populations used as references): A) Honey Creek Cave; B) Valdina Farms Sinkhole; C) Cascade Caverns system; and D) an undescribed structurally intermediate troglobitic *Eurycea* from Travis County, Texas. Filled diamonds indicate specimens collected in 1972-1974 in B) and since 1965 in C).

ence samples and the intermediate) the classification function of the analysis can evaluate the posterior probability that an individual belongs to its assigned population. All specimens of *E. neotenes* and *E. tridentifera* are properly allocated in these a posteriori tests, but eight individuals in the four intermediate samples are misclassified: one Honey Creek Cave specimen and three *E. troglodytes* sort with *E. tridentifera*, and one *E. troglodytes*, two *E. latitans* and one *E. sp.* are misclassified as *E. neotenes*. A reexamination of specimens misallocated as *E. tridentifera* refutes the possibility that they were initially misidentified, for they do not display the distinctive pigmentation or skull morphology (Potter and Sweet, 1981) of that species. In contrast, I cannot differentiate the remaining misclassified *E. troglodytes* and *E. latitans* from a sample of individuals representing several troglotic populations of *E. neotenes*.

If the reference samples alone are specified the individuals comprising the intermediate samples will be forced to sort with one or the other reference group on the basis of the simple majority of their affinities. This manipulation gives the following assignments (expressed as *E. tridentifera*: *E. neotenes*): Honey Creek Cave, 1:3; *E. troglodytes* 11:27; *E. latitans*, 2:17; and *E. sp.*, 0:32. As a further step, the *E. troglodytes* and *E. latitans* samples can be divided into three and two groups, respectively, on the basis of collection dates. The forced assortment of the two-group analysis reveals a clear trend in the affinities of the *E. troglodytes* subsamples: 1957, 7:8; 1967, 2:4, 1972–4, 1:13 (excluding three specimens, 1:2, of unknown collection date). The *E. latitans* material appears to show a similar trend: 1933–50, 2:7; post 1965, 0:10. Carrying this observation back to the three-group results, the four misclassified *E. troglodytes* include two 1957 and one 1967 as *E. tridentifera* and one 1972–4 specimen as *E. neotenes*. When the distributions of these subsamples in discriminant space are compared by multivariate analysis of variance the 1972–4 *E. troglodytes* collection is distinct from the 1957 and 1967 subsamples ($P < 0.01$); neither this latter pair nor the two *E. latitans* subsamples show significant differences in distribution.

The general conclusion from this analysis is that pre-1960 collections of *E. troglodytes* and *E. latitans* contain most of those individuals which closely resemble *E. tridentifera* (9 of 12 so assigned in the two-group tests and all three misclassified in the three-group tests), whereas more

recent samples of these species contain the majority of *E. neotenes*-like individuals (two-group, 27 of 42; three-group, 3 of 3). These results are difficult to explain except as the outcome of hybridization involving fluctuating numbers of *E. neotenes* and *E. tridentifera*-like individuals.

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, as least one is known (*E. sp.*). Further, only arguments by analogy can be advanced to counter the suggestion that increased levels of variability may actually 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 variation (see, for example, Jackson [1973] and Schueler and Rising [1976]). This evidence consists of discordant recombination of parental character states in hybrid individuals; it is perhaps the only unambiguous phenotypic evidence for hybrid origin of samples in which the presumed parental taxa are rare. Measures of individual variation 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 (W) 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 case 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 uniform rank across the set of characters. As 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 a measure of homogeneity among allometric relationships 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 combined.

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 4. 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. The significance of concordance values can be evaluated by transformation to chi-square (Siegel, 1956); all values save that of the Honey Creek Cave intermediate sample reflect highly significant association ($P < 0.01$) among the sets of rankings.

Comparison of Tables 2 and 4 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 the least homogeneous samples. *Eurycea latitans* is not differentiable from *E. neotenes* and *E. sp.* in the degree of association among character states.

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

TABLE 4. 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 Populations	N	Ties	Size range	W
<i>E. neotenes</i>				
Honey Creek Cave	6	0	17.0–31.6	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
<i>E. neotenes</i> × <i>tridentifera</i>				
Honey Creek Cave	4	0	29.0–37.8	0.12*
<i>E. latitans</i>				
Cascade Caverns system	17	0	9.5–47.8	0.74
<i>E. troglodytes</i>				
Valdina Farms Sinkhole	38	4	22.5–43.6	0.37
<i>E. sp.</i>				
Travis County	34	4	16.0–38.5	0.70
<i>E. tridentifera</i>				
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

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 hybrid sample (2:2) 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. However, the data from the type series are not entirely reliable, as Brandon (1971) has shown that the sex of the holotype was incorrectly determined.

DISCUSSION

While each of the three samples considered here can be distinguished from all other populations of the Texas *Eurycea* on grounds which suggest the occurrence of hybridization, the strength of this evidence varies among cases. The intermediate individuals in the Honey Creek Cave population are unequivocally of hybrid origin: all examined criteria agree, and the presumed parental taxa are sympatric. The criteria are also fully met in *E. troglodytes*, save that specimens clearly referable to *E. tridentifera* have not been collected in Valdina Farms Sinkhole. The 1972–74 sample from this site includes one specimen I am unable to distinguish from *E. neotenes* and several others which are very close

Note added in proof—*E. tridentifera* has been recently found in a second, smaller spring cave 1.2 km NE of Honey Creek Cave; *E. neotenes* is apparently absent at this site.

to that species in morphology. The weight of evidence favors the interpretation that *E. troglodytes* is a hybrid swarm of temporally unstable composition, in which the genetic influence of *E. tridentifera* has declined since 1957. Most individuals in the present population at Valdina Farms Sinkhole are predominantly similar to *E. neotenes*.

The evidence for hybrid influence is least conclusive in the case of *E. latitans*. This sample shows unusual heterogeneity in numbers of trunk vertebrae, high dispersion in discriminant space and contains two individuals which sort with *E. neotenes* in the discriminant classification. Nonetheless, the *E. latitans* sample displays levels of individual variation in allometric features (Table 2) and character concordance (Table 4) which are similar to those observed in other troglobitic populations of *E. neotenes*. The proximity of the known distributions of *E. latitans* and *E. tridentifera* in the maturely-developed cave systems of the Cibolo sinkhole plain lends plausibility to the interpretation that *E. latitans* represents a troglobitic population of *E. neotenes* which has incorporated a few individuals of *E. tridentifera* in the past. The present-day population in the Cascade Caverns system is not differentiable from four other populations of troglobitic *E. neotenes* widely scattered on the Edwards Plateau.

The taxonomic implications of these conclusions are as follows: *Eurycea troglodytes* Baker is an invalid taxon of hybrid origin, to be considered a junior synonym of *Eurycea neotenes* Bishop and Wright (part). The species name *trogodytes* remains available (I.C.Z.N., Article 17 (2)); it would replace *Eurycea tridentifera* Mitchell and Reddell if any member of the type series represented the same taxon as occurs at Honey Creek Cave. Data presented above eliminate this possibility: the holotype of *E. troglodytes* is a hybrid, as are the paratypes. To reflect this the synonymy of *E. tridentifera* should henceforth include the notation *Eurycea troglodytes* Baker (part). The same provisions apply to *Eurycea latitans* Smith and Potter, as a junior synonym of *E. neotenes* and an included name in the synonymy of *E. tridentifera*.

The partial or complete breakdown of reproductive isolation between *E. neotenes* and *E. tridentifera*, and the observed reproductive competence of the hybrids requires careful evaluation of the options for the continued recognition of *E. tridentifera*, either as a subspecies of

E. neotenes or as a distinct species. I prefer the latter alternative for the following reasons: 1) *E. tridentifera* is morphologically quite distinct from even the most highly cave-adapted populations of *E. neotenes*; 2) the range of *E. tridentifera* is wholly contained within the range of *E. neotenes* (Sweet, 1977a, 1982), though the two are seldom microsympatric; and 3) the two taxa appear to exhibit assortative mating where they occur in sympatry at Honey Creek Cave.

The last point requires some elaboration, and leads to a consideration of the factors responsible for the apparent breakdown of reproductive isolation in the populations known as *E. troglodytes* and *E. latitans*. One must also inquire as to how *E. latitans* has been able to maintain an intermediate level of troglobitic adaptation in a cave system otherwise inhabited by the advanced troglobite *E. tridentifera*.

Honey Creek Cave is an unusual site for *E. tridentifera* in that it opens as a flowing spring; all other localities for this species are deep sinkhole systems with no local outlet. *E. neotenes* occupies the spring at Honey Creek Cave, and as far as is known does not venture more than a few meters into the cave itself. The opportunity for ecological segregation of differently-adapted populations thus exists here, in contrast to the situation at Valdina Farms Sinkhole or in the Cascade Caverns system. Hybrid individuals would be expected to be at selective disadvantage in either the spring or deep cave habitats, thus favoring the development of reproductive isolating mechanisms in the parental taxa.

As a related point, it is interesting that spring-dwelling populations of *E. neotenes* are uncommon in the Guadalupe canyon in the vicinity of Honey Creek Cave. I examined 20 springs in this region, 15 of which were associated with caves, and found that 11 of the 12 populations of *E. neotenes* located were associated with caves (Sweet, 1978). In eight of these the populations are exclusively troglobitic, and are largely so in two others where individuals are only occasionally found in the spring habitat. Honey Creek Cave is the remaining site, and here *E. neotenes* is considerably more common in the spring than in the cave, despite the fact that observation and capture of salamanders is much more readily accomplished in the quiet waters of the cave. These observations are consistent with the suggestion that *E. neotenes* has been prevented from establishing a troglobitic population in Honey

Creek Cave by virtue of the presence of *E. tridentifera*.

Valdina Farms Sinkhole is located 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. 1). The intervening region is cavernous, but the caves are difficult of access and have been little explored. This is evidenced by the fact that the extensive cave survey program of the Texas Speleological Survey has produced no records of aquatic troglobites in this region (Reddell 1965, 1970). 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*; the latter 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 exclusion 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 I have seen in 1971, 1973 and 1974 during floods on Cibolo Creek. 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, 1967, 1971). 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, caves with fish are without populations of *Eurycea*, though some (such as Prassell Ranch Cave and Spring Creek Cave in the Guadalupe canyon) are apparently otherwise suitable, and are bracketed by fish-free caves inhabited by *Eurycea*. *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, pers. comm., 1976). 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, 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); 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.

The overall pattern of differentiation and secondary contact in troglobitic populations of the Texas *Eurycea* can be construed to support continued recognition of *E. tridentifera* and *E. neotenes* if the latter is expanded to include a variety of incipient and intermediate troglobitic populations into which the epigeal populations evenly grade. This is consistent with the general

model for the origin of troglobitic populations previously advanced (Sweet, 1977b; 1982). The currently recognized species *E. latitans* and *E. troglodytes* do not satisfy criteria for species status since both show evidence of hybrid origin or past influence. In both cases the populations now consist of individuals exhibiting a lesser degree of troglobitic specialization than was the case when they were discovered and described. In this connection it is significant that the period 1940–1956 was one of recurrent drought conditions throughout central Texas (Lowry, 1959); many springs and wells failed during this period (Brune, 1975), and it is likely that both the abundance of spring-dwelling salamanders and the distribution of troglobitic populations were altered in comparison to present conditions. These circumstances may have reduced the influx of epigeal *E. neotenes* at Valdina Farms Sinkhole in comparison to *E. tridentifera*, and would have resulted in a temporary absence of fish in the Cascade Caverns system, permitting occupancy by *E. tridentifera*. It is likely that both populations will continue to fluctuate in their composition in response to general climatic factors and the continued removal of groundwater from the Balcones Aquifer at a rate which exceeds its recharge capacity.

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