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Eurycea tridentifera, a New Species of Troglobitic Salamander from Texas and a Reclassification of *Typhlomolge rathbuni*

by ROBERT W. MITCHELL *and* JAMES R. REDDELL

Department of Zoology, The University of Texas

ABSTRACT

A new species of troglobitic salamander, *Eurycea tridentifera*, from the waters of Honey Creek Cave, Comal County, Texas, is described. The intermediate characteristics of this species and of *E. troglodytes* indicate that all the neotenic salamanders of the Edwards Plateau, *Eurycea* spp. and *Typhlomolge rathbuni*, constitute a closely related group of species. Differences between these species appear to be a function of adaptation to epigeal environments opposed to degree of adaptation to subterranean environments. Removal of *T. rathbuni* to *Eurycea* seems to reflect better the systematic relationships of these salamanders.

Convergent characteristics in the cavernicolous *Eurycea* are discussed, and several phenomena are recalled which, in addition to length of time of cave habitation, might affect the degree of cave-adaptation evident in the extant species. The first report of sympatry among the neotenic *Eurycea* is cited.

INTRODUCTION

The purpose of this paper is to present the description of a new species of troglobitic salamander from the subterranean waters of the Edwards Plateau of Texas and to demonstrate that the troglobitic salamander now known as *Typhlomolge rathbuni* should be removed to the genus *Eurycea*.

The diversity in the neotenic salamanders of the caves and spring-fed streams of the Edwards Plateau presents many interesting and demanding problems to students of systematics, distribution, speciation, and evolution. There are presently five described species of *Eurycea* and one of *Typhlomolge*. *Eurycea neotenes*, the first of the neotenic *Eurycea* to be described (Bishop and Wright, 1937), is the

most widely distributed species (Baker, 1961
several distinct salamanders are being referre
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and Potter, 1946, is known only from Cascad
hole, Dead Man's Cave, and Century Caver
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studies will reveal additional distinct species.

The new *Eurycea* described herein was t
Cave located near the small town of Spring B
This cave is a long water passage of which ap
been mapped (Reddell, 1964). Water tempe
water flow is about 100 gpm. There are two e
only one of which the stream issues.

METHODS

The salamanders were collected by hand
dip nets. They were immediately placed int
tainers of polystyrene foam for return to th
specimens taken were designated as the typ
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Jim Bogart of the University of Texas.

All linear measurements except eye dia
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ı to be described (Bishop and Wright, 1937), is the

most widely distributed species (Baker, 1961). It is quite possible that several distinct salamanders are being referred to this species. *Eurycea nana* Bishop, 1941, is apparently restricted to the spring-fed headwaters of the San Marcos River, Comal Co. *Eurycea latitans* Smith and Potter, 1946, is known only from Cascade Caverns, Cascade Sinkhole, Dead Man's Cave, and Century Caverns in Kendall Co.; caves which presumably share a common water system. *Eurycea pterophila* Burger, Smith, and Potter, 1950, appears to be restricted to Fern Bank Spring near the town of Wimberly, Hays Co. *Eurycea troglodytes* Baker, 1957, has been found only in the Valdina Farms Sinkhole, Medina Co. *Typhlomolge rathbuni* Stejneger, 1896, occurs only in the subterranean Purgatory Creek System, access to which is presently limited to Ezell's Cave located within the city limits of San Marcos, Texas. Of the preceding, *E. latitans* is a probable troglobite, while *E. troglodytes* and *T. rathbuni* are certainly troglobitic.

Some authors (Schmidt, 1953; Conant, 1958) have arbitrarily relegated various of these *Eurycea* to subspecific status, but until more comprehensive studies are made we prefer to regard each species distinct as originally described. Because of the existence of many isolated underground and epigeal stream systems, it is probable that future studies will reveal additional distinct species.

The new *Eurycea* described herein was taken from Honey Creek Cave located near the small town of Spring Branch, Comal Co., Texas. This cave is a long water passage of which approximately 400 m. have been mapped (Reddell, 1964). Water temperature is about 20°C, and water flow is about 100 gpm. There are two entrances to the cave from only one of which the stream issues.

METHODS

The salamanders were collected by hand and with the use of small dip nets. They were immediately placed into vacuum bottles or containers of polystyrene foam for return to the lab. Twenty of the 32 specimens taken were designated as the type series, and the remaining 12 were retained for physiological and behavioral study by Mr. Jim Bogart of the University of Texas.

All linear measurements except eye diameter were made to the nearest .1 mm with vernier calipers. Explanations of measurements are as follows: Total length—tip of snout to tip of tail (reported as sum of snout-vent and tail lengths). Snout-vent length—tip of snout to anterior margin of vent. Head length—tip of snout to posterior origin of third gill ramus; measured along a line parallel with antero-posterior axis of body. Axilla-groin length—posterior origin of forelimb to anterior origin of hindlimb. Tail length—anterior margin of vent to tip of tail. Snout length—tip of snout to imaginary line connecting anterior margins of eyes. Forelimb length—posterior origin of limb to tip of longest digit. Hindlimb length—anterior origin of limb to tip of longest digit. Head width—widest part of head. Body width—widest part of trunk. Forelimb width—greatest width at mid-portion of upper limb. Hindlimb width—greatest width at mid-portion of upper limb. Interorbital width—distance between the most medial margins of the eyes. Where appropriate all measurements were made on the left side.

Eye diameter was measured to the nearest .05 mm with an ocular micrometer mounted in a dissecting microscope. Measurement expresses greatest width of entire eye which was made easily visible by substage lighting.

Costal grooves were counted on each side and include only one in the axilla and two which may lie in close proximity in the groin. The costal groove overlap is that number of costal grooves included between the tips of the longest finger and toe of the adpressed limbs (left side only).

Only the premaxillary teeth were counted. The angles of the jaws were slit to facilitate opening of the mouth.

Sex was determined by viewing the gonads through a midventral incision.

Three specimens were stained with toluidine blue for study of the hyobranchial apparatus which was dissected from each.

Line drawings were initially made with the aid of a camera lucida attached to a dissecting microscope. The semi-diagrammatic head and dorsal views (Figs. 3 and 4) were subsequently modified to conform in their proportions, insofar as this was possible, to available mean values. This was done as a means of eliminating bias in each series of drawings since variation exists within each species. All head drawings were made approximately to the same center-of-eye to gular fold length and all dorsal views to the same snout-vent length to eliminate illusionary bias when viewing the illustrations.

RESULTS AND DISCUSSION

*Eurycea tridentifera** sp. nov.

Diagnosis. Neotenic. Gills pink to red with few minute flecks of

* L. *tridentifer*—a trident-bearer

dark pigment. Tongue free in front and for par
sides. Eyes about .6 mm in diameter, easily vi
within tissues of head, and with or without le
(11 in a single specimen). Extremities of a
overlapping and including about 2 (1–4) costal
Limbs attenuated, about 10 (8–13) times lon
1423 in order of increasing length; toes, 1524
for fingers, 2343; toes, 23443. Premaxillary te
(16–30) with numbers in the low 20's being r
palatine teeth series in the form of an inverted
interruption at midline and at about halfway
Head large, about 1/3 the snout-vent length an
of body by about 40%. Snout depressed abrup
truncated between external nares. Distance be
same as that between eyes. Cartilaginous ele
apparatus attenuated, especially the epibran
branchium trident-shaped, connected anterio
hyobranchium, and "S" shaped in lateral a
white in natural habitat, but grey pigment pre
pigment present in deeper lying tissues. Most
pattern, but a few have an indistinct reticul
dorso-lateral in tail, most dense near base, m
dorso-lateral in head.

Holotype. Sexually mature female (Figs. 1, 2
by James R. Reddell and Robert W. Mitchell
Comal Co., Texas, on Jan. 14, 1965. Total le
length, 37.0. Axilla-groin length, 18.2. Tail len
3.3. Forelimb length, 10.1. Hindlimb length,
Body width, 5.8. Forelimb width, 1.1. Hind
orbital width, 2.8. Right eye diameter, .45; left
12; overlap, 2. Premaxillary teeth, 23.

Holotype (USNM 153780), allotype (US
paratypes (USNM 153782–153785) have bee
National Museum; remainder of paratypes
deposited in the Texas Natural History Co
Texas, Austin, Texas. Paratypes TNHC 31
represented only by their disarticulated hyobr

Variation within the species. Tables 1 and
characters, absolute body measurements, r
measurements, and a statistical analysis of the
Table 2 shows that the ratios are quite const

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. Axilla-groin length—posterior origin of forelimb
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Holotype. Sexually mature female (Figs. 1, 2, and Cover). Collected by James R. Reddell and Robert W. Mitchell in Honey Creek Cave, Comal Co., Texas, on Jan. 14, 1965. Total length, 74.0. Snout-vent length, 37.0. Axilla-groin length, 18.2. Tail length, 37.0. Snout length, 3.3. Forelimb length, 10.1. Hindlimb length, 11.5. Head width, 1.3. Body width, 5.8. Forelimb width, 1.1. Hindlimb width, 1.3. Interorbital width, 2.8. Right eye diameter, .45; left eye, .40. Costal grooves, 12; overlap, 2. Premaxillary teeth, 23.

Holotype (USNM 153780), allotype (USNM 153781) and four paratypes (USNM 153782–153785) have been deposited in the U. S. National Museum; remainder of paratypes (TNHC 31521–31534) deposited in the Texas Natural History Collection, University of Texas, Austin, Texas. Paratypes TNHC 31525, 31530, and 31534 represented only by their disarticulated hyobranchia.

Variation within the species. Tables 1 and 2 give certain meristic characters, absolute body measurements, ratios of various body measurements, and a statistical analysis of the variation of these ratios. Table 2 shows that the ratios are quite constant regardless of size of

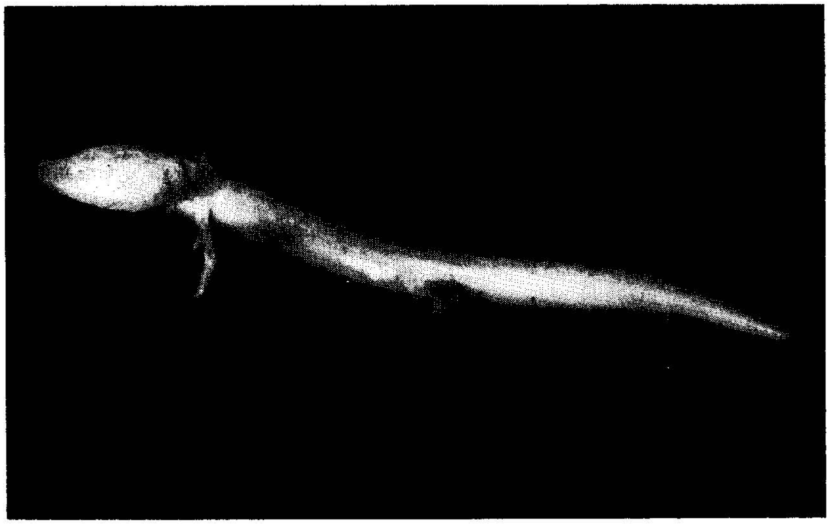

Fig. 1. Holotype of *Eurycea tridentifera* in life. Notice the large head, truncate snout, minute eyes, slight pigmentation, and attenuated lmbs.

the salamanders. Most of the standard errors of the mean ratios are less than 2% of the mean.

Comparisons with other species. The line drawings (Figs. 3 and 4) are intended to convey a general impression of the shape and proportional size of body parts obtaining in the neotenic salamanders of the Edwards Plateau. In general appearance, living specimens of *E. tridentifera* are somewhat similar to the other neotenic *Eurycea*, but the combination of large head, depressed snout, long, slender legs, and reduced eyes and pigmentation make this species readily distinguishable. It cannot be confused with *T. rathbuni*, which may be similarly characterized, because the angular head and the extremely long, slender legs of the latter make it one of the most distinctive of salamanders.

The posterior basibranchium is quite variable in these salamanders. In topotypes of *E. neotenes* it is lacking, in *E. nana* it is small and irregular in shape, in *E. pterophila* (Fig. 5) it is small and bi-radiating, in *E. latitans* and *E. troglodytes* it is larger and tri-radiating, and in none of these species is it connected anteriorly with the remainder of the hyobranchial apparatus (Burger, Smith, and Potter, 1950; Baker, 1957). It is quite well-developed in *E. tridentifera* and *T. rathbuni* and in each is connected anteriorly with the remainder of the hyobranchium (Fig. 5). In these latter two species that portion of the

Fig. 2. Holotype of *Eurycea tridentifera* in life. Notice
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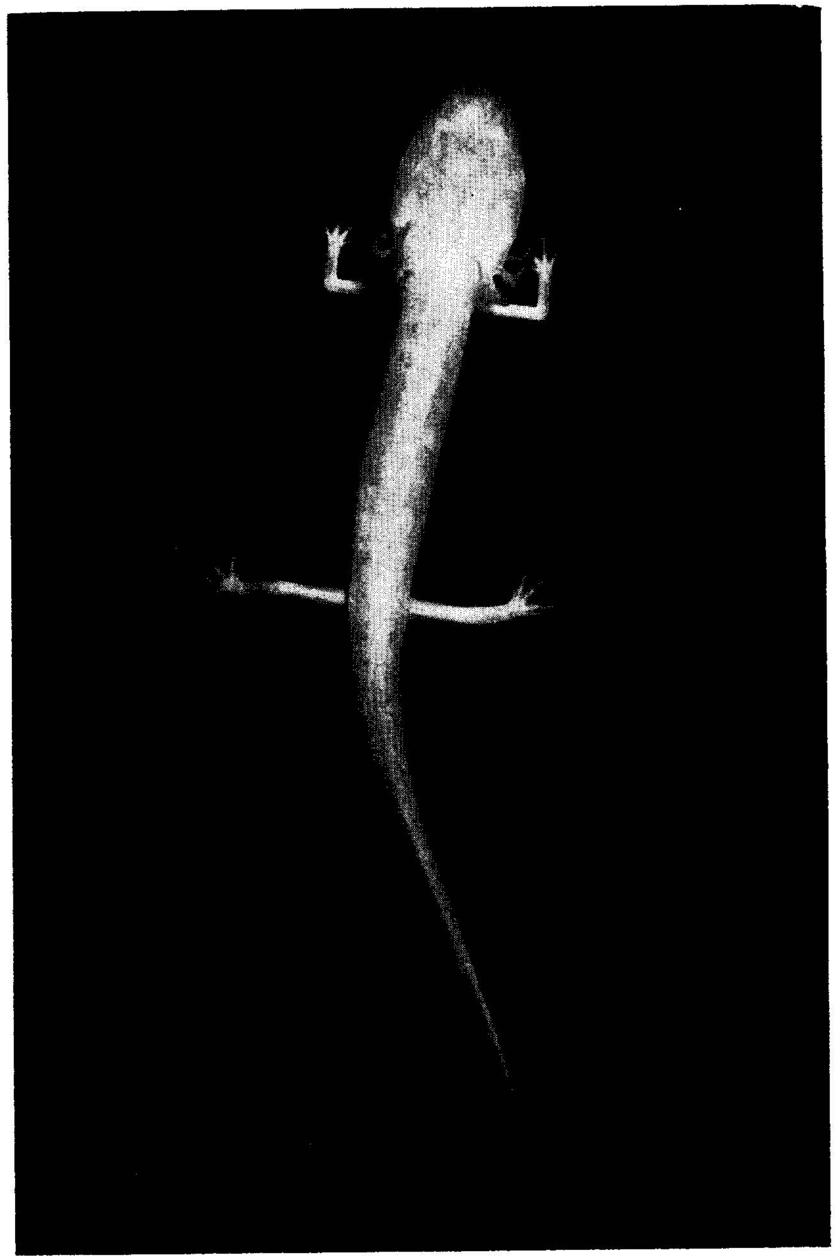

Fig. 2. Holotype of *Eurycea tridentifera* in life. Notice the depressed snout and minute eye.

TABLE 1

Sex, counts, and absolute body measurements of specimens in the type series of *Eurycea tridentifera*. SNo = specimen number. O = costal groove overlap. S = sex. PmT = number of premaxillary teeth. ToL = total length. SVL = snout-vent length. AGL = axilla-groin length. TaL = tail length. HeL = head length. SnL = snout length. FL = forelimb length. HiL = hindlimb length. HeW = head width. BW = body width. FW = forelimb width. HiW = hindlimb width. IoW = interorbital width. RED = right eye diameter. LED = left eye diameter. L = presence of lens. Measurements in mm. [1] measurements made on right side since left hindlimb was missing; tail partially amputated. [2] 11 costal grooves on each side; all others with 12.

SNo	S	O	PmT	ToL	SVL	AGL	TaL	HeL	SnL	FL	HiL	HeW	BW	FW	HiW	IoW	RED	LED
TNHC 31521	M	2	20	46.5	24.8	11.9	21.7	8.2	1.8	6.6	6.9	6.5	4.0	.6	.7	1.8	.65L	.65L
USNM 157382	F	1	30	61.2	31.9	16.0	29.3	10.4	2.8	8.3	8.9	7.3	4.5	.8	.9	2.3	.55L	.60L
TNHC 31522	M	1	16	55.6	30.4	14.6	25.2	10.0	2.8	7.3	7.9	6.7	4.8	.8	.9	2.3	.40	.55L
TNHC 31523	M	3	18	51.9	28.0	13.7	23.9	9.5	2.3	7.7	8.3	6.3	4.4	.7	.8	1.8	.65	.70L
TNHC 31524	F	1	22	54.4	28.3	15.2	26.1	9.7	2.3	7.5	8.8	6.3	4.2	.6	.7	2.0	.55	.80
USNM 157383	M	2	29	47.4	26.5	12.1	20.9	9.3	2.3	6.9	6.9	6.4	4.8	.8	.9	2.1	.70	.70
TNHC 31525	—	2	22	52.3	26.4	14.0	25.9	9.2	2.1	7.9	8.5	6.0	4.5	.7	.8	1.9	.70	.65
TNHC 31526	F	2	20	51.8	27.8	13.3	24.0	9.5	2.5	7.6	8.4	6.7	4.2	.6	.7	2.0	.55	.55
TNHC 31527	F	2	20	46.6	25.1	13.4	21.5	8.3	2.1	6.9	7.3	5.7	4.0	.7	.8	1.9	.55L	.55L
TNHC 31528	F	3	22	44.5	24.3	12.1	20.2	8.1	2.1	7.4	7.8	5.8	3.8	.7	.8	1.7	.60L	.60L
USNM 153781	M	2	16	44.0	23.7	12.6	20.3	7.8	1.9	6.3	7.5	5.2	3.7	.6	.7	1.4	.50L	.50L
TNHC 31529	F	2	22	43.0	22.8	11.3	20.2	7.8	1.9	6.3	6.9	5.3	3.9	.7	.7	1.8	.65L	.65L
TNHC 31530	—	1	18	35.8	19.4	9.9	16.4	6.7	1.5	5.4	5.9	4.4	3.2	.5	.6	1.5	.55	.55
TNHC 31531[1]	M	3	23	42.6	26.3	12.5	16.3	9.0	2.4	7.5	7.5	6.0	4.3	.8	.9	2.0	.75L	.80L
USNM 153784	M	4	20	42.2	22.5	10.4	19.7	8.1	2.0	6.6	7.4	5.4	3.6	.7	.8	1.6	.40	.60
TNHC 31532	M	2	22	63.9	34.0	16.4	29.9	12.1	3.6	9.2	10.0	8.2	5.6	1.0	1.1	2.9	.50	.55
TNHC 31533	F	2	20	42.4	22.3	11.0	20.1	7.9	1.8	6.0	7.3	5.3	3.9	.6	.7	1.6	.70L	.70
USNM 153780	F	2	23	74.0	37.0	18.2	37.0	12.9	3.3	10.1	11.5	8.9	5.8	1.1	1.3	2.8	.45	.40
TNHC 31534[2]	—	4	25	67.8	35.0	16.4	32.8	12.8	3.6	10.3	11.0	8.8	6.2	1.1	1.1	3.6	.70	.75
USNM 153785	F	4	20	39.2	21.3	10.7	17.9	7.6	1.7	6.1	6.8	5.2	3.4	.5	.6	1.7	.45	.50

TABLE 2

Ratios of selected body measurements of specimens in the type series of *Eurycea tridentifera*. $\bar{x}$ ED = mean diameter of the two eyes. Other symbols as explained Table 1. For statistical comparison of individuals with the type series use $\bar{x} \pm t$SD (95% confidence limits). For comparison of means of a series use $\bar{x} \pm t$SE (95% confidence limits). [1] not used in calculation of TaL % of SVL.

SNo	HeL % of SVL	TaL % of SVL	AGL % of SVL	FL % of SVL	HiL % of SVL	HeW % of SVL	BW % of SVL	HeW % of HeL	BW % of HeW	FW % of FL	HiW % of HiL	SL % of HeL	$\bar{x}$ED % of SVL	$\bar{x}$ED % of IoW	$\bar{x}$ED % of HeW
TNHC 31521	33.1	87.5	48.0	26.6	27.8	25.4	16.1	76.8	63.5	9.1	10.1	22.0	2.6	36.1	10.0
USNM 157382	32.6	91.8	50.2	26.0	27.9	22.9	14.1	70.2	61.6	9.6	10.1	26.9	1.8	25.0	7.9
TNHC 31522	32.9	82.9	48.0	24.0	26.0	22.0	15.8	67.0	71.6	11.0	11.4	28.0	1.6	20.7	7.1
TNHC 31523	33.9	85.4	48.9	27.5	29.6	22.5	15.7	66.3	69.8	9.1	9.6	24.2	2.4	37.5	10.7
TNHC 31524	34.3	92.2	53.7	26.5	31.1	22.3	14.8	64.9	66.7	8.0	8.0	23.7	2.4	33.8	10.7
USNM 157383	35.1	78.9	45.7	26.0	26.0	24.2	18.1	68.8	75.0	11.6	13.0	24.7	2.6	33.3	10.9
TNHC 31525	34.8	98.1	53.0	29.9	32.2	22.7	17.0	65.2	75.0	8.9	9.4	22.8	2.6	35.5	11.3
TNHC 31526	34.1	86.3	47.8	27.3	30.2	24.1	15.1	70.5	62.7	7.9	8.3	26.3	2.0	27.5	8.2
TNHC 31527	33.1	85.7	53.4	27.5	29.1	22.7	15.9	68.7	70.2	10.1	11.0	25.3	2.2	28.9	9.6
TNHC 31528	33.3	83.1	49.8	30.5	32.1	23.9	15.6	71.6	66.6	9.5	10.2	25.9	2.5	35.3	10.3
USNM 153781	32.9	85.7	53.2	26.6	31.6	21.9	15.6	66.7	71.2	9.5	9.3	24.4	2.1	35.7	9.6
TNHC 31529	34.2	88.6	49.6	27.6	30.3	23.3	17.1	67.9	73.6	11.1	10.1	24.4	2.9	36.1	12.3
TNHC 31530	34.5	84.5	51.0	27.8	30.4	22.7	16.5	65.7	72.7	9.3	10.1	22.4	2.8	36.7	12.5
TNHC 31531[1]	34.2	62.0	47.5	28.5	28.5	22.8	16.3	66.7	71.7	9.3	12.0	26.7	2.9	38.8	12.9

SNo	S	O	PmT	ToL	SVL	AGL	TaL	HeL	SnL	FL	HiL	HeW	BW	FW	HiW	IoW	RED	LED
TNHC 31521	M	2	20	46.5	24.8	11.9	21.7	8.2	1.8	6.6	6.9	6.5	4.0	.6	.7	1.8	.65L	.65L
USNM 157382	F	1	30	61.2	31.9	16.0	29.3	10.4	2.8	8.3	8.9	7.3	4.5	.8	.9	2.3	.55L	.60L
TNHC 31522	M	1	16	55.6	30.4	14.6	25.2	10.0	2.8	7.3	7.9	6.7	4.8	.8	.9	2.3	.40	.55L
TNHC 31523	M	3	18	51.9	28.0	13.7	23.9	9.5	2.3	7.7	8.3	6.3	4.4	.7	.8	1.8	.65	.70L
TNHC 31524	F	1	22	54.4	28.3	15.2	26.1	9.7	2.3	7.5	8.8	6.3	4.2	.6	.7	2.0	.55	.80
USNM 157383	M	2	29	47.4	26.5	12.1	20.9	9.3	2.3	6.9	6.9	6.4	4.8	.8	.9	2.1	.70	.70
TNHC 31525	—	2	22	52.3	26.4	14.0	25.9	9.2	2.1	7.9	8.5	6.0	4.5	.7	.8	1.9	.70	.65
TNHC 31526	F	2	20	51.8	27.8	13.3	24.0	9.5	2.5	7.6	8.4	6.7	4.2	.6	.7	2.0	.55	.55
TNHC 31527	F	2	20	46.6	25.1	13.4	21.5	8.3	2.1	6.9	7.3	5.7	4.0	.7	.8	1.9	.55L	.55L
TNHC 31528	F	3	22	44.5	24.3	12.1	20.2	8.1	2.1	7.4	7.8	5.8	3.8	.7	.8	1.7	.60L	.60L
USNM 153781	M	2	16	44.0	23.7	12.6	20.3	7.8	1.9	6.3	7.5	5.2	3.7	.6	.7	1.4	.50L	.50L
TNHC 31529	F	2	22	43.0	22.8	11.3	20.2	7.8	1.9	6.3	6.9	5.3	3.9	.7	.7	1.8	.65L	.65L
TNHC 31530	—	1	18	35.8	19.4	9.9	16.4	6.7	1.5	5.4	5.9	4.4	3.2	.5	.6	1.5	.55	.55
TNHC 31531[1]	M	3	23	42.6	26.3	12.5	16.3	9.0	2.4	7.5	7.5	6.0	4.3	.8	.9	2.0	.75L	.80L
USNM 153784	M	4	20	42.2	22.5	10.4	19.7	8.1	2.0	6.6	7.4	5.4	3.6	.7	.8	1.6	.40	.60
TNHC 31532	M	2	22	63.9	34.0	16.4	29.9	12.1	3.6	9.2	10.0	8.2	5.6	1.0	1.1	2.9	.50	.55
TNHC 31533	F	2	20	42.4	22.3	11.0	20.1	7.9	1.8	6.0	7.3	5.3	3.9	.6	.7	1.6	.70L	.70
USNM 153780	F	2	23	74.0	37.0	18.2	37.0	12.9	3.3	10.1	11.5	8.9	5.8	1.1	1.3	2.8	.45	.40
TNHC 31534[2]	—	4	25	67.8	35.0	16.4	32.8	12.8	3.6	10.3	11.0	8.8	6.2	1.1	1.1	3.6	.70	.75
USNM 153785	F	4	20	39.2	21.3	10.7	17.9	7.6	1.7	6.1	6.8	5.2	3.4	.5	.6	1.7	.45	.50

TABLE 2

Ratios of selected body measurements of specimens in the type series of *Eurycea tridentifera*. $\bar{x}$ ED = mean diameter of the two eyes. Other symbols as explained Table 1. For statistical comparison of individuals with the type series use $\bar{x} \pm t$SD (95% confidence limits). For comparison of means of a series use $\bar{x} \pm t$SE (95% confidence limits). [1] not used in calculation of TaL % of SVL.

SNo	HeL % of SVL	TaL % of SVL	AGL % of SVL	FL % of SVL	HiL % of SVL	HeW % of SVL	BW % of SVL	HeW % of HeL	BW % of HeW	FW % of FL	HiW % of HiL	SL % of HeL	$\bar{x}$ED % of SVL	$\bar{x}$ED % of IoW	$\bar{x}$ED % of HeW
TNHC 31521	33.1	87.5	48.0	26.6	27.8	25.4	16.1	76.8	63.5	9.1	10.1	22.0	2.6	36.1	10.0
USNM 157382	32.6	91.8	50.2	26.0	27.9	22.9	14.1	70.2	61.6	9.6	10.1	26.9	1.8	25.0	7.9
TNHC 31522	32.9	82.9	48.0	24.0	26.0	22.0	15.8	67.0	71.6	11.0	11.4	28.0	1.6	20.7	7.1
TNHC 31523	33.9	85.4	48.9	27.5	29.6	22.5	15.7	66.3	69.8	9.1	9.6	24.2	2.4	37.5	10.7
TNHC 31524	34.3	92.2	53.7	26.5	31.1	22.3	14.8	64.9	66.7	8.0	8.0	23.7	2.4	33.8	10.7
USNM 157383	35.1	78.9	45.7	26.0	26.0	24.2	18.1	68.8	75.0	11.6	13.0	24.7	2.6	33.3	10.9
TNHC 31525	34.8	98.1	53.0	29.9	32.2	22.7	17.0	65.2	75.0	8.9	9.4	22.8	2.6	35.5	11.3
TNHC 31526	34.1	86.3	47.8	27.3	30.2	24.1	15.1	70.5	62.7	7.9	8.3	26.3	2.0	27.5	8.2
TNHC 31527	33.1	85.7	53.4	27.5	29.1	22.7	15.9	68.7	70.2	10.1	11.0	25.3	2.2	28.9	9.6
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USNM 153781	32.9	85.7	53.2	26.6	31.6	21.9	15.6	66.7	71.2	9.5	9.3	24.4	2.1	35.7	9.6
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TNHC 31531[1]	34.2	62.0	47.5	28.5	28.5	22.8	16.3	66.7	71.7	9.3	12.0	26.7	2.9	38.8	12.9
USNM 153784	36.0	87.6	46.2	29.3	32.9	24.0	16.0	66.7	66.7	10.4	10.8	24.7	2.2	31.3	9.3
TNHC 31532	35.6	87.9	48.2	27.1	29.4	24.1	16.5	67.5	68.3	10.9	11.0	30.0	1.5	18.1	6.4
TNHC 31533	35.4	90.1	49.3	26.9	32.7	23.8	17.5	67.1	73.6	10.0	9.6	22.8	3.1	43.8	13.2
USNM 153780	34.9	100.0	49.2	27.3	31.1	24.1	15.7	69.0	65.2	10.9	11.3	25.6	1.1	15.2	4.8
TNHC 31534[2]	36.6	93.7	46.9	29.4	31.4	25.1	17.7	68.8	70.5	10.7	10.0	28.1	2.1	20.1	8.2
USNM 153785	35.7	84.1	50.2	28.6	31.9	24.4	16.0	68.4	65.4	8.2	8.8	22.4	2.2	27.9	9.1
$\bar{x}$	34.4	88.1	49.5	27.5	30.1	23.4	16.2	68.2	69.1	9.8	10.2	25.1	2.3	30.9	9.8
tSD	2.41	11.01	4.98	3.18	4.21	2.09	2.05	5.59	8.60	2.26	2.55	4.52	1.07	15.99	4.65
tSE	.54	2.52	1.11	.71	.94	.46	.46	1.26	1.93	.50	.57	1.00	.23	3.58	1.05

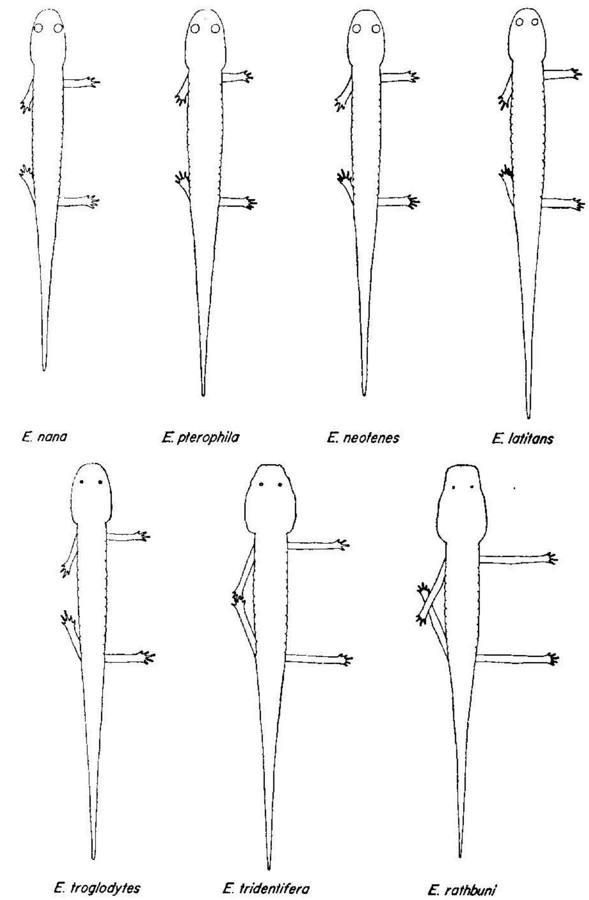


Fig. 3. Outlines in dorsal aspect of the neotenic salamanders of the Edwards Plateau. Notice especially the gradation in body part proportions.

posterior basibranchium which corresponds to the whole of the basibranchium in the former five species is bi-radiating in *T. rathbuni* and tri-radiating in *E. tridentifera*. *Eurycea tridentifera* is immediately separable from the other neotenic salamanders of the Plateau by its characteristic posterior basibranchium.

The number of costal grooves in *E. tridentifera*, 12, is less than in any of the other Plateau *Eurycea* (*E. troglodytes*, 13–14; *E. latitans*, 14–15; *E. neotenes*, 15–16; *E. pterophila*, 15–16; *E. nana*, 16–17) and is the same as in *T. rathbuni*. Of the five previously known Plateau *Eurycea*, only in *E. troglodytes* do the extremities of the adpressed

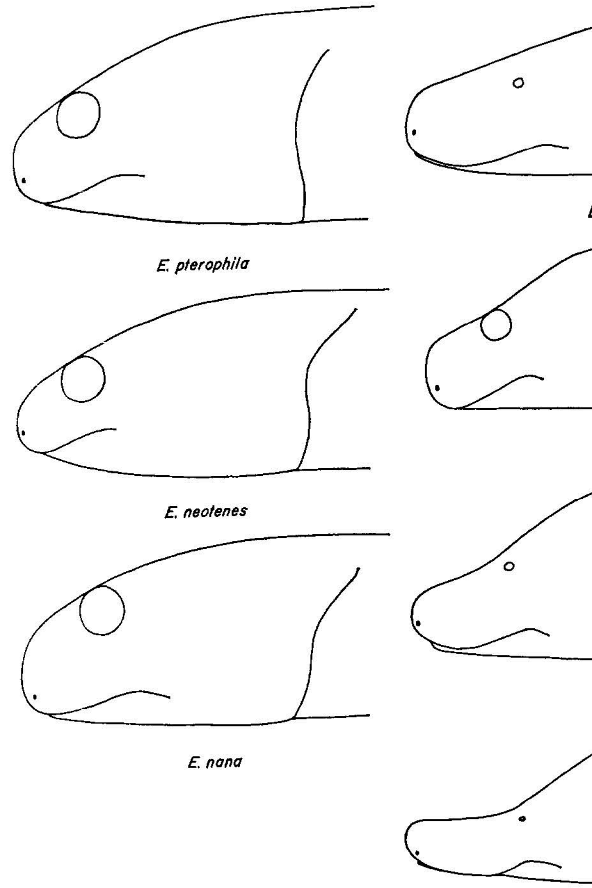
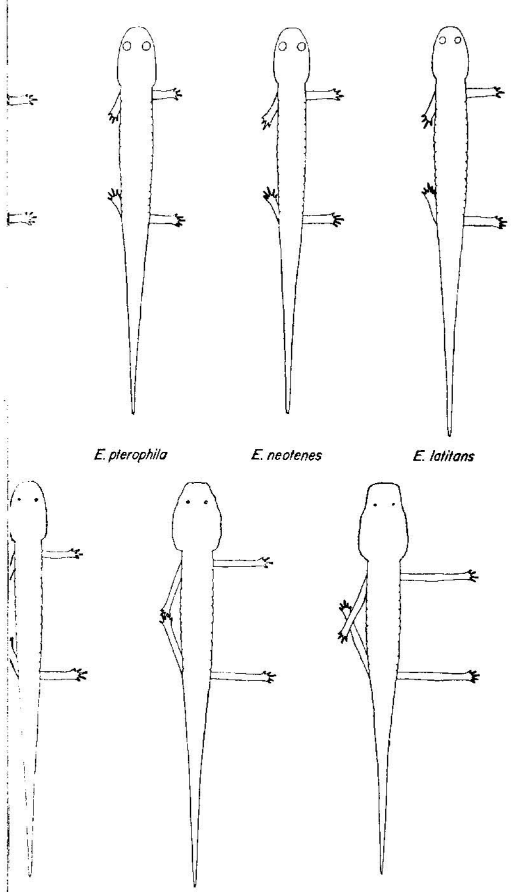


Fig. 4. Outlines of heads of the neotenic salamanders of the I

limbs touch, and even this is rare since usuall grooves separate the adpressed limbs in this specie attentuation in *T. rathbuni* results in an overlap attenuation in *E. tridentifera* is intermediate *troglodytes* and *T. rathbuni*.

The eyes of *E. tridentifera* are intermediate in s *E. troglodytes* and *T. rathbuni*. They are more va those of *E. troglodytes* and only about half possess does not mention the lenses of *E. troglodytes*, bu



n dorsal aspect of the neotenic salamanders of the Edwards Plateau. gradation in body part proportions.

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of costal grooves in *E. tridentifera*, 12, is less than in Plateau *Eurycea* (*E. troglodytes*, 13–14; *E. latitans*, nes, 15–16; *E. pterophila*, 15–16; *E. nana*, 16–17) and n *T. rathbuni*. Of the five previously known Plateau n *E. troglodytes* do the extremities of the adpressed

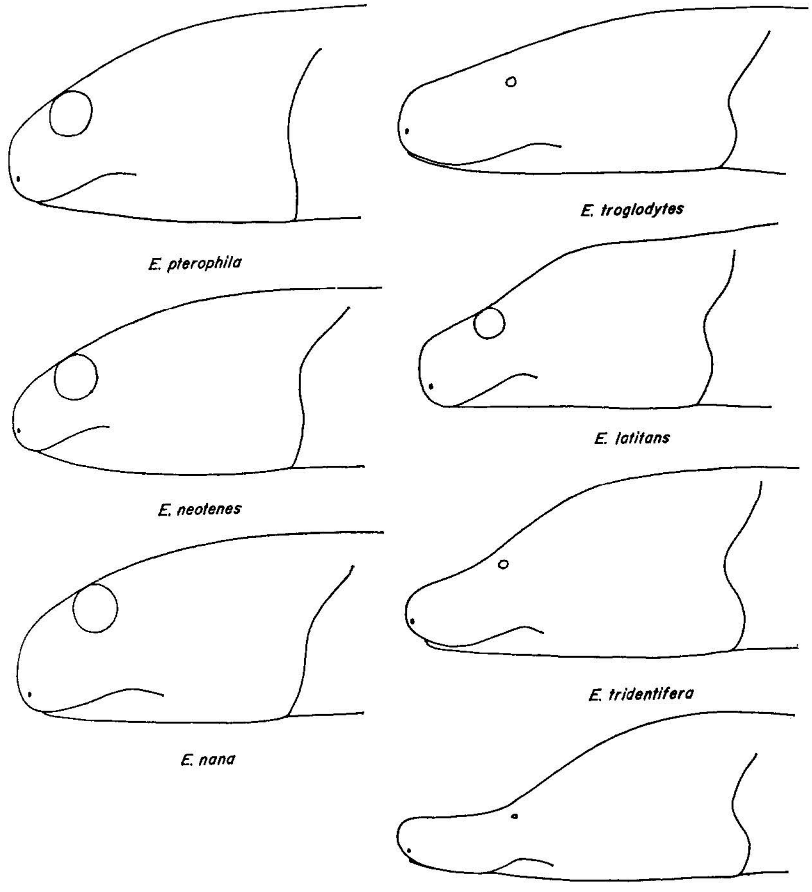

Fig. 4. Outlines of heads of the neotenic salamanders of the Edwards Plateau.

limbs touch, and even this is rare since usually about two costal grooves separate the adpressed limbs in this species. The extreme limb attentuation in *T. rathbuni* results in an overlap of about six. Limb attenuation in *E. tridentifera* is intermediate between that of *E. troglodytes* and *T. rathbuni*.

The eyes of *E. tridentifera* are intermediate in size between those of *E. troglodytes* and *T. rathbuni*. They are more variable in shape than those of *E. troglodytes* and only about half possess lenses. Baker (1957) does not mention the lenses of *E. troglodytes*, but of 11 specimens of

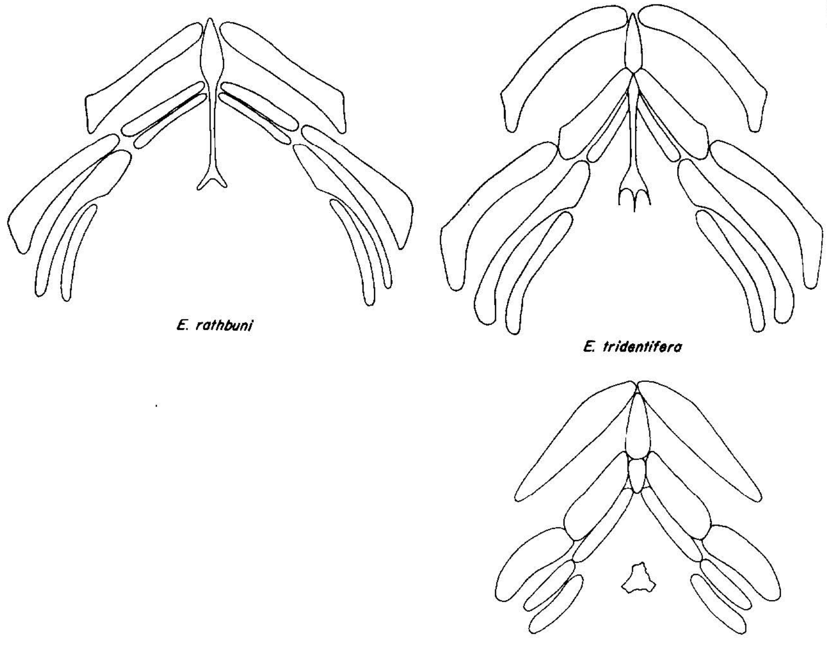

Fig. 5. Hyobranchia of three neotenic salamanders of the Edwards Plateau. *E. rathbuni* after Hilton, 1945. *E. pterophila* after Burger, Smith, and Potter, 1950.

his type series available to us, none had eyes lacking in lenses. The eyes of *T. rathbuni* lack lenses.

The depigmentation in *E. tridentifera* is exceeded only by that of *T. rathbuni*. *Eurycea troglodytes* and *E. latitans* are also depigmented but less so than the former two species.

The number of premaxillary teeth in *E. tridentifera* is greater than in *E. nana*, *E. pterophila*, *E. neotenes*, and *E. latitans*, but less than in *E. troglodytes* and *T. rathbuni*. The configuration of the vomeropalatine teeth series is similar in these species as is the tongue shape and attachment.

Head width in *E. tridentifera* exceeds that in any of the other Plateau *Eurycea* and is about the same as that in *T. rathbuni*. The head of *T. rathbuni*, however, is longer. In its truncated snout and separation of external nares *E. tridentifera* is intermediate between *E. troglodytes* and *T. rathbuni*. Snout depression in *E. tridentifera* is intermediate between that in *E. latitans* and the extreme depression in *T. rathbuni*. The head of *E. troglodytes* is gently sloping and does not

have the abrupt depression at eye level characte
three species. The anterior part of the head in dorsa
tridentifera and *T. rathbuni* is of the same gene
except for the more angular nature of that in the la

The affinities of Eurycea *and* Typhlomolge. B
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The fact that characteristics in evidence in vari
of neotenic *Eurycea* combine in their extreme in *T*
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be sufficient justification for continued separation

Emerson (1905) has pointed out in great detail t
blances between skeletal characteristics of *T. rat*
Pseudotriton ruber (*Spelerpes ruber* at the time of
states that the main differences between these two
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nificance of this comparison for our purposes lies in
larity of skeletal characteristics of larval *Pseudo*
Eurycea. The generically diagnostic skeletal char
1926) between these latter two genera arise at met

Because of the apparent lack of good qualitativ
fact that the obvious differences are ones of degree
geographic proximity of the species, we suggest
salamanders of the Edwards Plateau are, in fact,
group of species descended from a common ancest
ences within the group are evidently a function of
selection pressures between the subterranean and
ments. We, therefore, see no justification in the r
lomolge as a valid genus and propose that the
Eurycea rathbuni (Stejneger) reflects more accura
relationships of this salamander.

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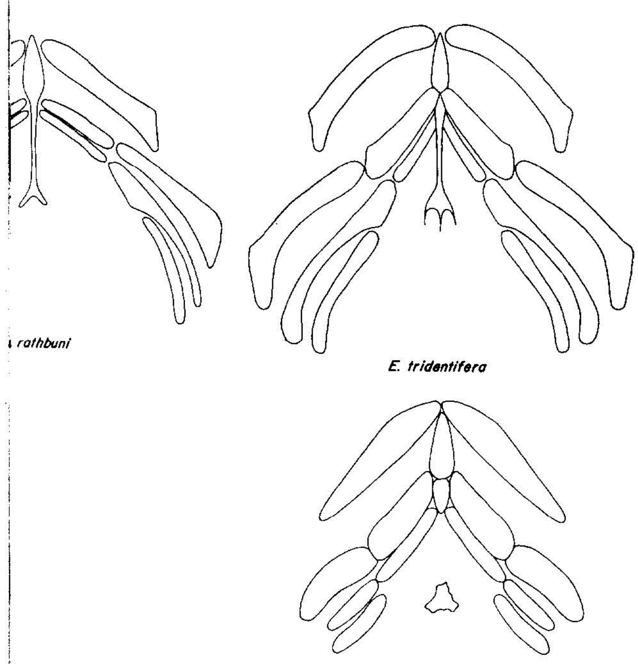

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have the abrupt depression at eye level characterizing the former three species. The anterior part of the head in dorsal aspect of both *E. tridentifera* and *T. rathbuni* is of the same general configuration except for the more angular nature of that in the latter.

The affinities of Eurycea *and* Typhlomolge. Baker (1957) has mentioned the intermediate nature of *E. troglodytes* between the neotenic surface forms of *Eurycea* and *T. rathbuni*, and he states that *E. troglodytes* "demonstrates a way that *Typhlomolge* could have evolved from a *Eurycea*-type ancestor." *Eurycea tridentifera* provides a further and even more striking demonstration that the differences between the neotenic *Eurycea* and *T. rathbuni* are almost wholly ones of degree only.

The fact that characteristics in evidence in various of the species of neotenic *Eurycea* combine in their extreme in *T. rathbuni* to produce an emergent facies unique among salamanders does not seem to be sufficient justification for continued separation of the two genera.

Emerson (1905) has pointed out in great detail the striking resemblances between skeletal characteristics of *T. rathbuni* and larval *Pseudotriton ruber* (*Spelerpes ruber* at the time of her writing). She states that the main differences between these two salamanders are the reduced eyes and greatly attenuated limbs of *T. rathbuni*. The significance of this comparison for our purposes lies in the further similarity of skeletal characteristics of larval *Pseudotriton* and larval *Eurycea*. The generically diagnostic skeletal characteristics (Dunn, 1926) between these latter two genera arise at metamorphosis.

Because of the apparent lack of good qualitative differences, the fact that the obvious differences are ones of degree only, and the close geographic proximity of the species, we suggest that the neotenic salamanders of the Edwards Plateau are, in fact, a closely related group of species descended from a common ancestor. Present differences within the group are evidently a function of the differences in selection pressures between the subterranean and epigeal environments. We, therefore, see no justification in the retention of *Typhlomolge* as a valid genus and propose that the new combination *Eurycea rathbuni* (Stejneger) reflects more accurately the systematic relationships of this salamander.

There are many genera of animals in which are included "epigeum-adapted" and "cave-adapted" species all related by similar basic structure and presumably common ancestry. The highly divergent appearances of the species within these genera reflect their adaptation to vastly different habitats, not their lack of close relationship. Some excellent examples of this phenomenon are obvious in the isopod genus *Asellus*, the beetle genera *Rhadine* and *Batrisodes*, the millipede genus *Cambala*, the spider genera *Cicurina*, *Leptoneta*, and *Nesticus*, the ostracod genus *Candona*, the crayfish genera *Procambarus*, *Cambarus*, and *Orconectes*, the shrimp genus *Palaemonetes*, and the amphipod genera *Crangonyx* and *Gammarus*.

Convergence in the cavernicolous Eurycea *of the Edwards Plateau.* The cavernicolous *Eurycea* of the Plateau share several characteristics by which they differ from their epigeal relatives. Moreover, there is a gradation in these characteristics, each becoming more pronounced, with few exceptions, in the order *E. latitans*, *E. troglodytes*, *E. tridentifera*, and *E. rathbuni*. We, as Baker (1957), emphasize that these graded characters should not be taken to indicate that any of the extant species are ancestral to others. Each species has, undoubtedly, evolved independently of the other since the original colonization of the subterranean water system by the ancestral form. Present similarities in these species are more likely the products of convergent evolution resulting from at least gross similarities in the major selection pressures in the underground water systems. These convergent characteristics are reduction in quantity and quality of the eye, pigment reduction, increase in tooth number, decrease in number of costal grooves, limb attenuation, increase in head size, snout depression, snout truncation, greater separation of external nares, and increase in size of the posterior basibranchium. Any attempt to explain the adaptive nature of most of these characteristics would be wholly within the realm of speculation.

The degree of adaptation to the subterranean environment. All too often in the literature dealing with cave animals those of a certain group which are the most highly modified are presumed to be the oldest; i.e., to have entered the subterranean environment prior to their less modified relatives. We should like to point out that while time is exceedingly important, evolutionary rates must not be overlooked. It is quite possible, for example, that these cave-adapted *Eurycea* of the Edwards Plateau entered their underground environments at approximately the same time and that their differences in appearance have resulted from selection pressures of different intensities. Not only may the selection pressures differ quantitatively, but they may also differ qualitatively, and each may vary independently through time. In addition, the extent to which the gene pool of the evolving troglobite is diluted by epigeal invaders not yet reproduc-

tively isolated would affect greatly the length of t high degree of adaptation. Also important is change a phenomenon especially important in caves whe tend to be small. The frequency, degree, and du population levels could affect greatly the time requ new characteristics in the population.

Sympatry in the neotenic Eurycea. Baker (19 Edwards Plateau as inhabited by many endemic a lations of neotenic salamanders (sic). Until now t reported instances of sympatry among the Plateau in Honey Creek Cave there is another *Eurycea* in *dentifera*. The single specimen which we collected in the *neotenes* complex. This specimen was taken the spring entrance, well beyond the nearest dist trance where several specimens of *E. tridentifera* individuals of apparently this same species have be the entrance and outside the cave among the roc water flows before entering Honey Creek (William

In no other cave in which troglobitic *Eurycea* h is the subterranean water system directly and perm with an epigeal stream through the cave entrance. I to assume that the epigeal stream has been popula least as long as has the subterranean stream since th of entry into the cave by colonizers would be the e tion of the epigeal stream has been uninterrupted, t to be a distinct possibility that ecological isolating important in the evolution of *E. tridentifera*.

It is also possible that the subterranean stream cently bisected by Honey Creek and that invasi species occurred after the evolution of E. *tridentifera*

SUMMARY

A new species of troglobitic salamander, *Eurycea* the waters of Honey Creek Cave, Comal Co., Texas intermediate characteristics of this salamander toge *E. troglodytes* provide strong evidence that all manders of the Edwards Plateau, *Eurycea* spp. *rathbuni*, constitute a closely related group of s between these species appear to be a function of ad environments opposed to degree of adaptation to sub

s of this phenomenon are obvious in the isopod genus genera *Rhadine* and *Batrisodes*, the millipede genus der genera *Cicurina*, *Leptoneta*, and *Nesticus*, the *ndona*, the crayfish genera *Procambarus*, *Cambarus*, ne shrimp genus *Palaemonetes*, and the amphipod and *Gammarus*.

the cavernicolous Eurycea *of the Edwards Plateau.* *Eurycea* of the Plateau share several character-ney differ from their epigeal relatives. Moreover, n in these characteristics, each becoming more pro-exceptions, in the order *E. latitans*, *E. troglodytes*, l *E. rathbuni*. We, as Baker (1957), emphasize that cters should not be taken to indicate that any of the ancestral to others. Each species has, undoubtedly, ntly of the other since the original colonization of ater system by the ancestral form. Present similari-s are more likely the products of convergent evolu-at least gross similarities in the major selection derground water systems. These convergent charac-ion in quantity and quality of the eye, pigment in tooth number, decrease in number of costal nuation, increase in head size, snout depression, reater separation of external nares, and increase in basibranchium. Any attempt to explain the adap-of these characteristics would be wholly within ation.

aptation to the subterranean environment. All too are dealing with cave animals those of a certain ne most highly modified are presumed to be the entered the subterranean environment prior to relatives. We should like to point out that while important, evolutionary rates must not be over-possible, for example, that these cave-adapted ards Plateau entered their underground environ-ately the same time and that their differences in ulted from selection pressures of different intensi-the selection pressures differ quantitatively, but qualitatively, and each may vary independently dition, the extent to which the gene pool of the s diluted by epigeal invaders not yet reproduc-

tively isolated would affect greatly the length of time required for a high degree of adaptation. Also important is change in population size, a phenomenon especially important in caves where population sizes tend to be small. The frequency, degree, and duration of very low population levels could affect greatly the time required for fixation of new characteristics in the population.

Sympatry in the neotenic Eurycea. Baker (1957) describes the Edwards Plateau as inhabited by many endemic and allopatric populations of neotenic salamanders (sic). Until now there have been no reported instances of sympatry among the Plateau *Eurycea*. However, in Honey Creek Cave there is another *Eurycea* in addition to *E. tridentifera*. The single specimen which we collected evidently belongs in the *neotenes* complex. This specimen was taken about 25 m inside the spring entrance, well beyond the nearest distance from the entrance where several specimens of *E. tridentifera* were taken. Other individuals of apparently this same species have been seen just inside the entrance and outside the cave among the rocks over which the water flows before entering Honey Creek (William Russell, per. com.)

In no other cave in which troglobitic *Eurycea* have been reported is the subterranean water system directly and permanently connected with an epigeal stream through the cave entrance. It seems reasonable to assume that the epigeal stream has been populated by *Eurycea* at least as long as has the subterranean stream since the most likely point of entry into the cave by colonizers would be the entrance. If habitation of the epigeal stream has been uninterrupted, there would appear to be a distinct possibility that ecological isolating mechanisms were important in the evolution of *E. tridentifera*.

It is also possible that the subterranean stream has been only recently bisected by Honey Creek and that invasion by the epigeal species occurred after the evolution of E. *tridentifera*.

SUMMARY

A new species of troglobitic salamander, *Eurycea tridentifera*, from the waters of Honey Creek Cave, Comal Co., Texas, is described. The intermediate characteristics of this salamander together with those of *E. troglodytes* provide strong evidence that all the neotenic salamanders of the Edwards Plateau, *Eurycea* spp. and *Typhlomolge rathbuni*, constitute a closely related group of species. Differences between these species appear to be a function of adaptation to epigeal environments opposed to degree of adaptation to subterranean environ-

ments. The removal of *T. rathbuni* to *Eurycea* seems to better reflect the systematic relationships of these salamanders.

The convergent characteristics in the cavernicolous *Eurycea* are discussed. Several phenomena are recalled which, in addition to addition of time of cave habitation, might affect the degree of cave adaptation evident in the extant species. The first reported instance of sympatry among these neotenic *Eruycea* is cited for *E. tridentifera* and a member of the *E. neotenes* complex.

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