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A NEW SPECIES OF SUBTERRANEAN BLIND SALAMANDER (PLETHODONTIDAE: HEMIDACTYLIINI: *EURYCEA*: *TYPHLOMOLGE*) FROM AUSTIN, TEXAS, AND A SYSTEMATIC REVISION OF CENTRAL TEXAS PAEDOMORPHIC SALAMANDERS

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ABSTRACT: We describe a new species of salamander (*Eurycea*) from the Barton Springs segment of the Edwards Aquifer, Austin, Texas, USA. The new species is most closely related to *Eurycea* (*Typhlomolge*) *rathbuni* from subterranean waters around San Marcos, Texas, and like that species lacks external eyes and shows other morphological features associated with subterranean life. The new species is easily distinguished on the basis of morphology from all previously described species of salamanders, and in particular is easily distinguished from its closest relatives, *E.* (*Typhlomolge*) *rathbuni* and *E.* (*Typhlomolge*) *robusta*, as well as the sympatric *E. sosorum*. We used sequences of the mitochondrial cytochrome *b* gene to infer the phylogeny of described species of central Texas *Eurycea*, and these data support the major groups reported previously on the basis of other DNA and allozyme data. We also define names for the major clades of central Texas *Eurycea*.

Key words: Caudata; Plethodontidae; Hemidactyliini; *Eurycea waterlooensis* new species; *Blepsimolge* new clade; *Notiomolge* new clade; *Paedomolge* new clade; *Septentriomolge* new clade; *Typhlomolge* clade definition; *Eurycea* clade definition; Endangered species; Texas; Barton Springs

"[*Eurycea neotenes*] was described in September, 1937, on the basis of nine specimens taken in April, 1936, from Culebra Creek, 5 miles north of Helotes, Bexar County, Texas . . . . This is a very interesting discovery; and surprising, since no small area in Texas has been more carefully collected over than that about Helotes. Gabriel Marnock made of it an historic region that many herpetologists have visited as a shrine; yet so evident an animal as this salamander had escaped notice until 1936." L. T. Murray (1939:5)

MANY distinct species of paedomorphic salamanders from the springs and caves of the Edwards Plateau in central Texas have been overlooked by generations of herpetologists. The first member of this group to be described was *Eurycea* (*Typhlomolge*) *rathbuni*, which was collected from an artesian well at the Federal Fish hatchery in San Marcos, Texas in the 1890s (Stejneger, 1896). However, the first surface species of paedomorphic salamander described from central Texas, *Eurycea neotenes*, was not discovered at Helotes until 1936 (Bishop and Wright, 1937; see also quote above by L. T. Murray), and somehow herpetologists missed the abundant *Eurycea nana* (sympatric with *E. rathbuni* at San Marcos Springs) until 1938 (Bishop, 1941). Both of these localities were visited by numerous herpetologists for many years prior to the discovery of these common animals. Perhaps even more surprising is the case of *Eurycea sosorum* from Barton Springs, in downtown Austin, Texas. Despite the fact that dozens of herpetologists received the Ph.D. from the 1940s to the 1990s at The University of Texas at Austin, this species was not described until 1993 (Chippindale et al., 1993).

For several years prior to the initial petitions to list *Eurycea sosorum* as a federal Endangered Species in 1992, cleaning practices at Barton Springs had reduced most of the observable population of salamanders to a small number of individuals around the main spring outlet (Parthenia Spring). Changes in cleaning practices (elimination of the use of chlorine, and the reduction in mechanical disturbance and the use of high-pressure hoses) from 1992–1997 (when the species was formally listed as Endangered) resulted in some recovery of the population. The biggest threat to the continued existence of this species now comes from development of the recharge zone of the Barton Springs segment of the Edwards Aquifer, which has resulted in some new decline of the population (especially from increased siltation of the aquifer and springs). Nonetheless, efforts to protect *Eurycea sosorum* allowed some recovery of the species in the mid-1990s from the extremely small population sizes that resulted from earlier cleaning practices in the pool area. The City of Austin has protected one of the outlets of Barton Springs (Sunken Gardens Spring) as a salamander refuge since 1998, and the city plans to restore another outlet (Eliza Spring) to a more natural state that is expected to benefit salamander populations. Prior to its protection, Sunken Gardens Spring was heavily affected by humans, who often used the spring for bathing and even washing clothes, and most of Eliza Spring was encased in concrete in the early 1900s.

Since the description of *Eurycea sosorum,* there have been occasional sightings of juveniles of a morphologically distinct paedomorphic salamander at Barton Springs that resembles *E.* (*Typhlomolge*) *rathbuni* more than *E. sosorum.* However, given the Endangered status of *Eurycea sosorum,* collection of salamanders at Barton Springs has been closely regulated and restricted. Combined with the fact that this second species is only very rarely seen at the surface, and typically only juveniles are seen in the spring outlets, obtaining sufficient material for its description has been difficult. However, we have now verified that a parallel situation exists between Barton Springs and San Marcos Springs. In each case, there are two species of salamanders: one surface species with functional image-forming eyes (*E. sosorum* at Barton Springs and *E. nana* at San Marcos Springs) and one blind subterranean species (an undescribed species at Barton Springs and *E. rathbuni* at San Marcos Springs). Here we name the new species from Barton Springs.

METHODS

We sequenced copies of the mitochondrial cytochrome *b* gene from individuals of all the described species of central Texas *Eurycea* (except for *Eurycea robusta,* which is known only from the holotype; see Appendix I for a listing of specimens). We amplified a 1026–1141 bp fragment of the mitochondrial cytochrome *b* gene using the forward primer MVZ15 (GAACTAATGGCCCACACWWTACGNAA; Moritz et al., 1992) and the reverse primer HEMTHRREV (CTTTGRCTTACAAGGYCAATG) or EURCB9 (GATTGAGGAYRCTTGTCCAATTTC). We used standard PCR conditions (Palumbi, 1996) with annealing temperatures of 45–52 C and extension times of 1–1.5 min, and standard automated sequencing protocols (Li-Cor and PE Biosystems). Phylogenetic analyses were performed using the MVZ15-EURCB9 fragment (1026 bp). Phylogenetic analyses (parsimony and maximum-likelihood criteria) were conducted using PAUP* (v4.b4, Swofford, 1998). An exact solution for the parsimony analysis (with equal character weighting) was found using the branch-and-bound search algorithm. The maximum-likelihood analysis was based on the GTR+Γ+INV model of sequence evolution (Swofford et al., 1996). Rate heterogeneity was modeled using four evolutionary rate classes, including an invariant class. For the maximum likelihood analysis, we performed heuristic searches (TBR branch swapping) on five stepwise addition trees based on random taxon addition. We conducted 500 bootstrap replicates for parsimony and 100 bootstrap replicates for maximum likelihood analyses (Felsenstein, 1985).

Measurements were made with digital calipers to the nearest 0.1 mm. Measurements used to compare species included total length (TL: tip of snout to tip of tail), standard length (SL: tip of snout to posterior margin of cloaca), axilla–groin length, trunk width (at maximum point between axilla and groin), width of the upper

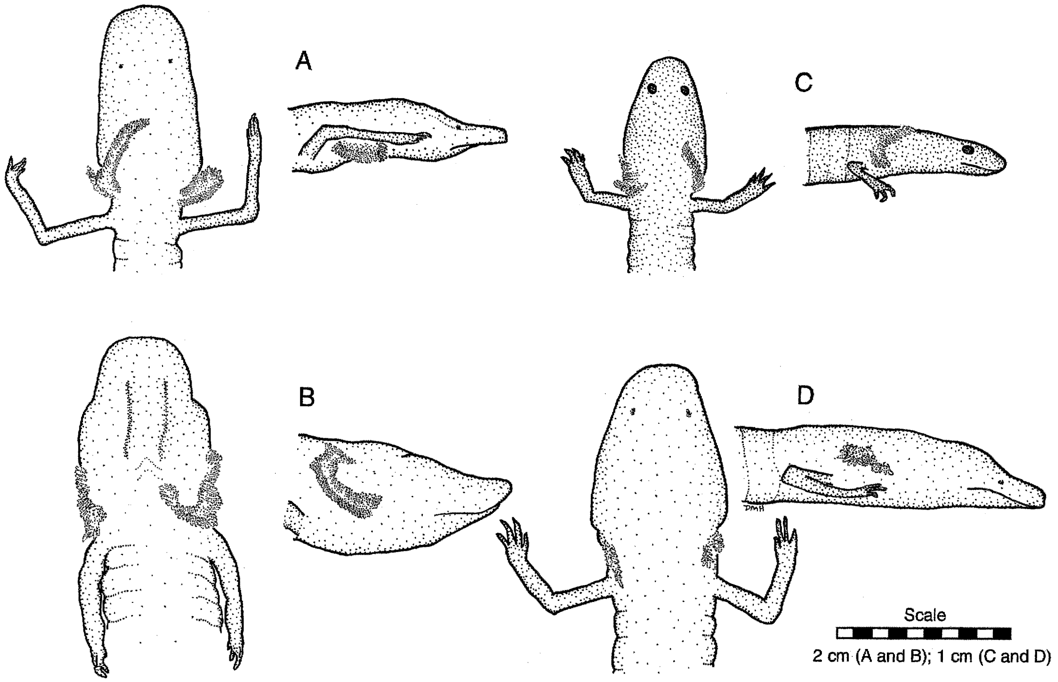

FIG. 1.—Comparison of the dorsal and lateral aspects of the heads and forelimbs of (A) *Eurycea rathbuni* (TNHC 51175, from Rattlesnake Cave, Hays Co., Texas); (B) *E. robusta* (TNHC 20255, holotype); (C) *E. sosorum* (TNHC 51184, holotype); and (D) *E. waterlooensis* (TNHC 60201, holotype). Note that (A) and (B) are at 0.5× scale compared to (C) and (D).

forelimb (at maximum), head width at eyes, maximum head width, height of the dorsal and ventral tail fins at mid-tail, and height of the caudal musculature at mid-tail.

SPECIES DESCRIPTION

Eurycea ***waterlooensis*** sp. nov.

Holotype.—TNHC 60201 (Fig. 1D), collected 13 January 1998 by Robert Hansen and Dee Ann Chamberlain from Sunken Gardens Spring (Fig. 2), an outlet of Barton Springs, Zilker Park, Austin, Travis Co., Texas. This individual was a juvenile (27.5 mm total length) when captured, but was raised in captivity until 13 November 1998 (to a total length of 68.6 mm), when the distal 2-mm of its tail was removed for molecular analysis and the specimen was preserved.

Paratypes.—TNHC 60202, collected 22 January 1999 from the type locality and preserved 16 December 1999 (total length = 62.5 mm); TNHC 60203, a juvenile (total length = 18.0 mm) collected 3 May 1999 from Barton Springs Pool, Zilker Park, Austin, Travis Co., Texas; and TNHC 60320, a juvenile (total length = 13.0 mm) collected 27 August 1998 from Eliza Spring, Zilker Park, Austin, Travis Co., Texas. All specimens of this species have been collected by employees of the City of Austin's Watershed Protection Department (Robert Hansen and Dee Ann Chamberlain) under a permit issued by the United States Fish and Wildlife Service (Endangered Species Permit TE 833851).

Etymology.—In 1837 or 1838, Mirabeau Buonaparte Lamar, then Vice President of the Republic of Texas, went in search of a new site for the capital city on the western frontier of the Republic. He found a site along the Colorado River inhabited by Joseph Harrell on the north bank of the river, and William and Stacy

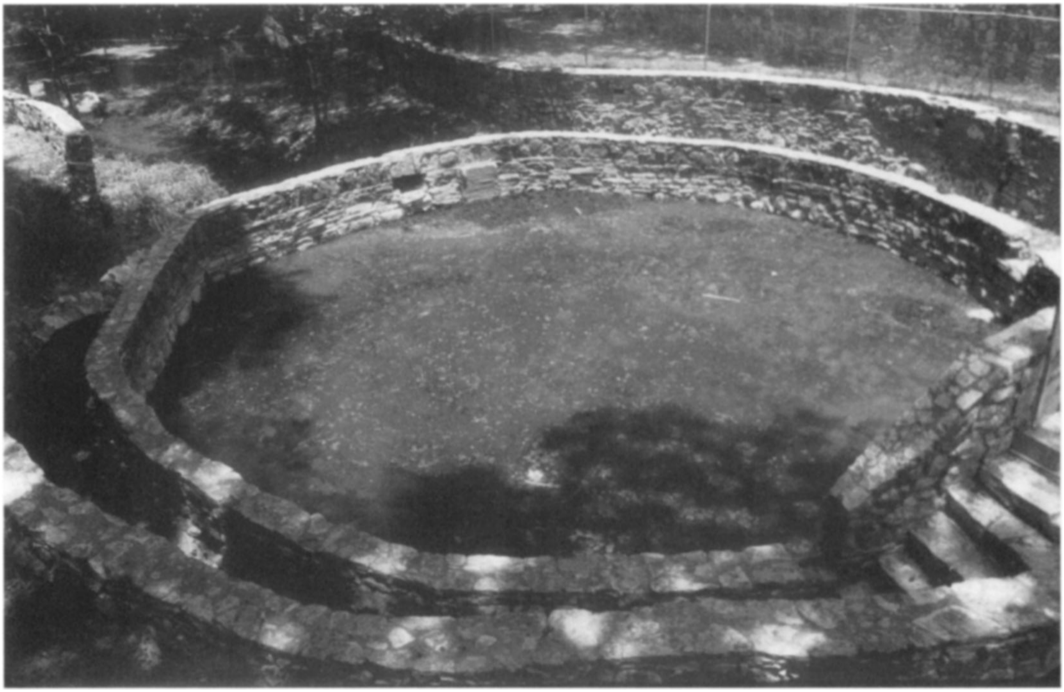

FIG. 2.—Sunken Gardens Spring salamander refuge, the type locality of *Eurycea waterlooensis*.

Barton, who had settled on the south bank of the river around what would become known as Barton Springs. When Lamar became President of the Republic of Texas in December 1838, he directed a commission to visit the site, and in January 1839 they selected the site for the new capital and named it Waterloo. The Congress of Texas changed the name of the city to Austin. *Eurycea waterlooensis*, therefore, is named after the original name of Austin, Texas, whose citizens have long protected Barton Springs for its natural beauty, its clean, cool water, and its unique biological diversity. We recommend that this species be known by the common name of Austin Blind Salamander.

Diagnosis.—Eurycea waterlooensis is easily distinguished from all other species of *Eurycea* by the following combination of morphological characters. (1) *Eurycea waterlooensis* is perennibranchiate, which distinguishes it from most species of *Eurycea* from outside the Edwards Plateau region of central Texas. (2) External eyes are absent (there are no lenses, and the dark eye spots that are present are covered by undifferentiated skin). The dark eye spots are superficially indistinguishable from those in *E. rathbuni*, whereas the vestigial eye spots of *E. robusta* are proportionally smaller and less visible (Fig. 1). Other described species of *Eurycea* typically have external eyes with well developed lenses, although lenses are absent in some specimens of *E. tridentifera* (the dark eye spots are proportionally much larger in *E. tridentifera* than in *E. waterlooensis, E. rathbuni*, or *E. robusta*). We call *E. waterlooensis* a "blind salamander," following the practice with *E. rathbuni* and *E. robusta*, because all three species lack image-forming lenses. However, all three species do have small eye spots below the surface of the skin (presumably homologous with the pigment layer of the retina), and may be able to detect the presence or absence of light. (3) There are 12 costal grooves in *E. waterlooensis*, as in *E. robusta* and *E. rathbuni*. Most other species of paedomorphic *Eurycea* have 13 or more costal grooves. Most specimens of the sympatric *E. sosorum* have 14–15 costal grooves, although Chippindale et al. (1993) reported single specimens of this species with 13 and 16 costal grooves. (4) The limbs of *E. waterlooensis* are proportionally much shorter than in *E. rathbuni* or *E. robusta.* The adpressed limbs of *E. rathbuni* overlap by 5–9 costal folds; those of the single specimen of *E. robusta* overlap by one costal fold; and the adpressed limbs of *E. waterlooensis* are separated by 1–3 costal folds. (5) The tail fins of *E. waterlooensis* are weakly developed; the ventral portion of the tail fin is present only on the posterior half of the tail, and the dorsal portion is very low or absent on the anterior half of the tail. In contrast, most other species of paedomorphic *Eurycea* (including the closest relatives *E. rathbuni* and *E. robusta,* as well as the sympatric *E. sosorum*) typically have well-developed tail fins that are distributed along the entire length of the tail (although fin development is somewhat variable in *E. sosorum*). At mid-tail, the relative proportions of the heights of the dorsal tail fin, the caudal musculature, and the ventral tail fin are approximately 0.31–0.54–0.15 in the holotype of *E. robusta,* 0.26–0.60–0.14 in specimens of *E. rathbuni,* and 0.05–0.95–0.0 in the holotype of *E. waterlooensis.*

In general appearance and coloration, *E. waterlooensis* is most similar to *E. rathbuni* and *E. robusta.* These three species share a lateral expansion of the anterior cranial elements that produce an extended snout (Fig. 1). *Eurycea rathbuni* and *E. waterlooensis* (and presumably *E. robusta,* which we have not seen in life) have a reflective, pearly white appearance which apparently results from the transparent skin and the underlying reflective connective tissues. However, specimens of *E. waterlooensis* show more pigmentation than either *E. rathbuni* or *E. robusta,* and live specimens of *E. waterlooensis* exhibit a translucent or reflective lavender coloration in the dorsal skin above the pearly white luster, a result of a light but nearly uniform distribution of melanophores in the skin. In addition, some specimens of *E. waterlooensis* exhibit a distinct row of iridophores along each side of the body and tail. The only adult specimen of *E. waterlooensis* collected in the wild appears somewhat darker in coloration (the lavender appearance is more strongly developed) compared to the juveniles of this species, or compared to the adults that have been raised in captivity. *Eurycea waterlooensis* can also be distinguished from *E. rathbuni* and *E. robusta* by its much shorter limbs (see above) and by proportional differences in head and body shape. The head, body, and limbs of *E. robusta* are much thicker and heavier than in either *E. waterlooensis* or *E. rathbuni.* The trunk width is 45.8% of the axilla–groin length in the single specimen of *E. robusta,* compared to 34.5% in 10 specimens of *E. rathbuni* measured by Potter and Sweet (1981), and 30.3% in the holotype of *E. waterlooensis.* The width of the upper forelimb is 19.1% of the forearm length in *E. robusta,* compared to 7.4% in *E. rathbuni* and 11.4% in *E. waterlooensis.* The head of *E. rathbuni* is nearly as wide at the eye spots as at its widest point (just in front of the gills), whereas in *E. waterlooensis* and *E. robusta,* the head is markedly narrower at the eye spots than at the widest point in front of the gills (Fig. 1). As described above, the tail fins of *E. waterlooensis* are much more weakly developed than in *E. rathbuni* or *E. robusta.* The hind digits of *E. waterlooensis* also differ from both *E. rathbuni* and *E. robusta* in relative length; the hind digits of *E. waterlooensis* are 4-3-2-5-1 in order of decreasing length, whereas in the other two species the digits are 3-4-2-5-1. The gills on the known specimens of *E. waterlooensis* are also proportionally smaller than in either *E. robusta* or *E. rathbuni* (Fig. 1).

All known specimens of *E. waterlooensis* are smaller than adults of *E. rathbuni* or *E. robusta,* although *E. waterlooensis* grows considerably larger than *E. sosorum.* The largest preserved specimen of *E. waterlooensis* (the holotype) has a standard length (SL) of 35.6 mm and total length (TL) of 66.6 mm (68.6 mm before the tail tip was removed), and the largest living specimen in captivity was approximately 81 mm TL in December 2000. In contrast, the holotype of *E. robusta* has a SL of 57.1 mm and TL of 100.8 mm, and 10 specimens of *E. rathbuni* measured by Potter and Sweet (1981) had a mean SL of 56.1 mm and TL of 100.9 mm. Five specimens of *E. waterlooensis* maintained alive in captivity grew rapidly for ~8 mo from ~15 mm to ~60 mm TL, after which growth slowed to ~1 mm/mo; we conclude from these observations that individuals likely reach sexual maturity at about 60 mm TL. The only adult of *E. waterlooensis* collected in the wild was 66 mm TL.

The only known species of aquatic salamander that is sympatric with *Eurycea waterlooensis* is *E. sosorum* (Fig. 3). These two species are easily distinguished by the lack of external eyes and the pronounced extension of the snout in *E. waterlooensis* (Figs. 1, 3), as well as its smaller number of costal grooves (12, versus 13–16 in *E. sosorum*). Coloration of *E. sosorum* is typically darker than in *E. waterlooensis*, with varying degrees of dorsal blotching and mottling produced from an irregular pattern of melanophores, with areas of high concentrations of silvery-white iridophores. In contrast, *E. waterlooensis* exhibits the overall pearly white luster also seen in *E. rathbuni*, apparently the result of the light-reflective connective tissue that underlies the skin. There is a relatively uniform but light distribution of melanophores across the dorsal surfaces of the head, body, and tail of *E. waterlooensis* (ventral surfaces are unpigmented). In addition, there are typically a few spots of highly reflective iridophores along the side of the body of *E. waterlooensis*, and a higher concentration of these spots on the tail.

Description of the holotype.—Standard length: 35.6 mm; total length: 66.6 mm (68.6 mm before tail tip was removed); snout to gular fold: 8.6 mm; snout to base of third gill ramus: 11.9 mm; eye spot to base of third gill ramus: 8.5 mm; width of head at level of the jaw articulation: 7.3 mm; diameter of eye spots: 0.45 mm; distance between eye spots: 3.1 mm; maximum trunk width: 5.7 mm; axilla–groin length: 18.8 mm; forelimb length: 8.8 mm; upper forelimb width: 1.0 mm; hindlimb length: 11.2 mm; upper hindlimb width: 1.5 mm; tail length: 32.7 mm (34.7 mm before removal of the tail tip).

There are 12 costal grooves, although the anterior-most and posterior-most costal grooves are very weakly developed, so that only 10 costal grooves are readily apparent. There are four digits on the forelimbs, 3-2-4-1 in order of decreasing length, and five digits on the hindlimbs, 4-3-2-5-1 in order of decreasing length. The snout is elongate and flattened, and the body is flattened ventrally. The tail fins are weakly developed and clearly evident only on the posterior half of the tail.

In life, the overall appearance of the holotype was pearly white with a light lavender hue, with lightly pigmented skin and a few lateral highly reflective white spots formed by iridophores, which were more concentrated on the tail. In the preserved specimen, small dark eye spots are evident, but they are buried deep beneath the skin. The dorsal surfaces of the head, body, and tail are covered with a relatively uniform distribution of melanophores at a density of approximately 25/mm^2. There are a few light colored spots, lacking in melanophores, that correspond to the location of the reflective iridophores that were evident in life. The ventral surfaces of the head and body are almost completely lacking melanophores, and in life the heart and other internal organs were visible through the skin. The gills were bright red in life.

Variation.—The paratypes are similar to the holotype in most respects, although TNHC 60202 is darker overall. TNHC 60203 and 60320 are juveniles, in which the eye spots appear proportionally larger in relation to the head than in the adults; the tail fins are proportionally larger in the juvenile specimens as well. Six additional specimens are currently maintained alive in captivity by the City of Austin; as of December 2000, these specimens were 81 mm, 80 mm, 68 mm, 66 mm, 50 mm, and 30 mm in total length. The live specimens resemble the other known specimens, although the largest specimen collected from the wild (66 mm) is the darkest individual. The light dorsolateral islands of

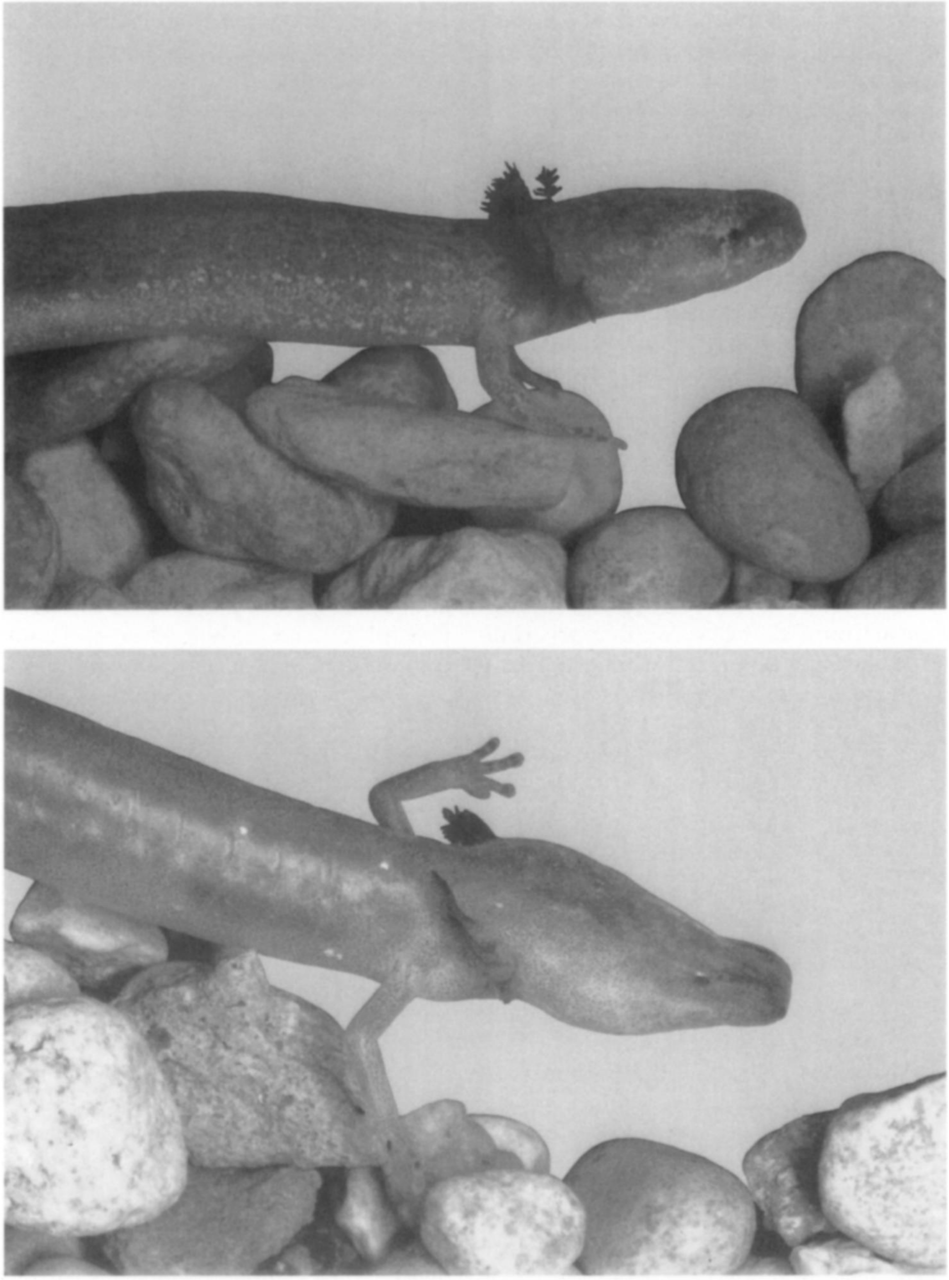

FIG. 3.—Comparison of the sympatric species *Eurycea sosorum* (top) and *E. waterlooensis* (bottom). Both of these specimens are part of the captive breeding program for these species administered by the City of Austin.

iridophores in three of the living specimens are present as pairs of light spots extending along each side of the back, and these spots are more numerous and concentrated on the tail. Tail fin development is somewhat variable among the known specimens, although all have weakly developed tail fins in comparison to *E. rathbuni* or *E. robusta*. In most of the specimens, there is a very shallow dorsal tail fin that extends to near the base of the tail, but the ventral tail fin does not extend anterior to the mid-point of the tail.

Distribution and natural history.—This species has been observed at three of the four outlets of Barton Springs: Parthenia (Main) Spring, which forms Barton Springs Pool (photograph in Chippindale et al., 1993); Eliza Spring (photograph in Chippindale et al., 1993); and Sunken Gardens (Old Mill) Spring (Fig. 2). To date, *E. sosorum* is the only species of salamander that has been observed at the Upper Spring outlet of Barton Springs. City of Austin employees have conducted a monthly salamander census of the four outlets of Barton Springs from 1997 to the present. During the period of July 1998–December 2000 (when records of *E. sosorum* and *E. waterlooensis* were differentiated), 1535 salamanders were observed (many of these probably represent repeat observations in different months), of which 1518 were *E. sosorum* and only 17 were *E. waterlooensis.* However, these observations are likely a reflection of the respective habitats of the two species: *E. sosorum* is primarily a surface species, whereas *E. waterlooensis,* like its relative *E. rathbuni,* is probably mostly restricted to subterranean cavities of the Edwards Aquifer. All but one of the specimens of *E. waterlooensis* observed in the springs have been juveniles, which likely were flushed out of the aquifer accidentally. Of the 18 documented observations of *E. waterlooensis* (the 17 observations from July 1998–December 2000 plus the holotype collected in January 1998), 14 were at Sunken Gardens Spring, three in the main pool (Parthenia Spring), and one in Eliza Spring. Specimens of *E. waterlooensis* have been observed throughout much of the year, although 12 of 18 observations were in the winter months of November, December, and January, and four of the remaining observations were in the mid-summer months of July and August (the two remaining observations were in February and May).

The wild-caught adult specimen of *E. waterlooensis* defecated the remains of amphipods, ostracods, copepods, and plant material after it was brought into captivity. In captivity, this species feeds readily on a wide variety of small aquatic invertebrates.

As part of the recovery efforts for the endangered *Eurycea sosorum,* the City of Austin is developing a captive breeding program for the species. This program also now includes *E. waterlooensis,* and six of the known individuals are currently maintained alive as part of this program. Disturbances associated with human activities in Barton Springs Pool are probably less likely to affect *E. waterlooensis* than *E. sosorum,* although both species are negatively affected by changes in the Barton Springs segment of the Edwards Aquifer that result from development in the recharge and contributing zones of the aquifer. In particular, the rapidly increasing levels of siltation in Barton Springs and the aquifer seen over the past decade are a cause for concern regarding the continued existence of these two species.

Captive specimens of *E. waterlooensis* often crawl out of the water onto the sides of an aquarium, where they use the side of their flattened muscular tails to adhere to the wet surface of the glass. Individuals spend many minutes at a time out of water if humidity is near 100%.

PHYLOGENETIC RELATIONSHIPS AND HIGHER TAXONOMY

Our inferred phylogeny of the central Texas paedomorphic salamanders based on cytochrome *b* sequences is shown in Fig. 4. There was a single best maximum-likelihood solution (Fig. 4), and four equally short parsimony trees. The four parsimony solutions differed among themselves in the relationships among *E. tridentifera, E. latitans, E. pterophila,* and *E. neotenes,* although one of the four solutions for these taxa was identical to the maximum likelihood tree shown in Fig. 4. In addition, each of the parsimony trees switched the positions of *E. chisholmensis* and *E. naufragia* compared to the maximum likelihood tree. However, all the deeper branches of the tree were the same in both analyses, and most of the major groups were supported by high bootstrap proportions in both analyses (Fig. 4). Among the

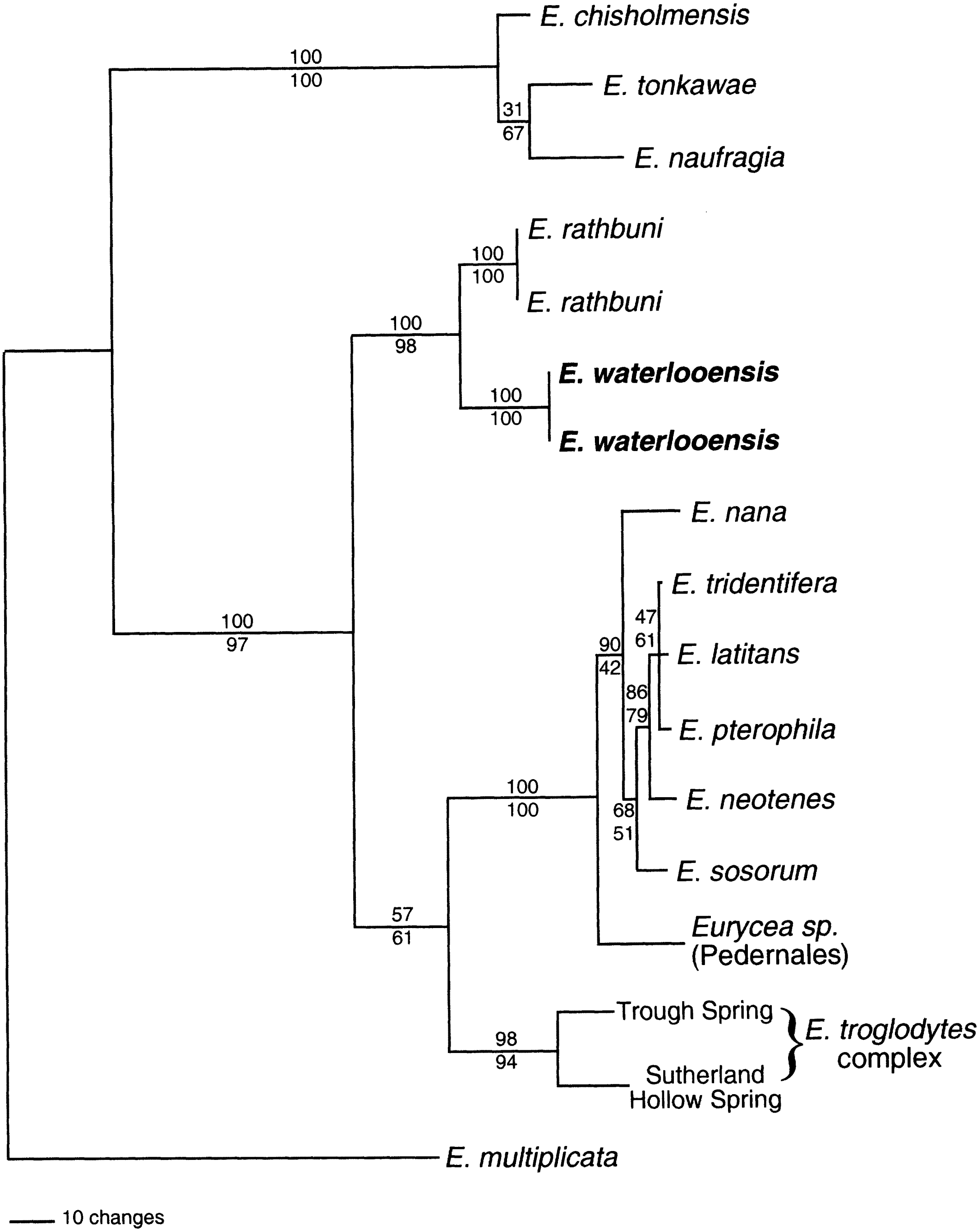

FIG. 4.—Phylogenetic relationships of the central Texas clade of paedomorphic *Eurycea*, based on sequences of the cytochrome *b* gene (museum voucher numbers and GenBank accession numbers are given in Appendix I). The branching topology of the tree shown is based on the best maximum likelihood solution; branch lengths are based on character reconstructions under parsimony. The numbers adjacent to branches indicate bootstrap support for the respective clades, with bootstrap values for the parsimony analysis shown on top and bootstrap values for the maximum likelihood analysis shown below.

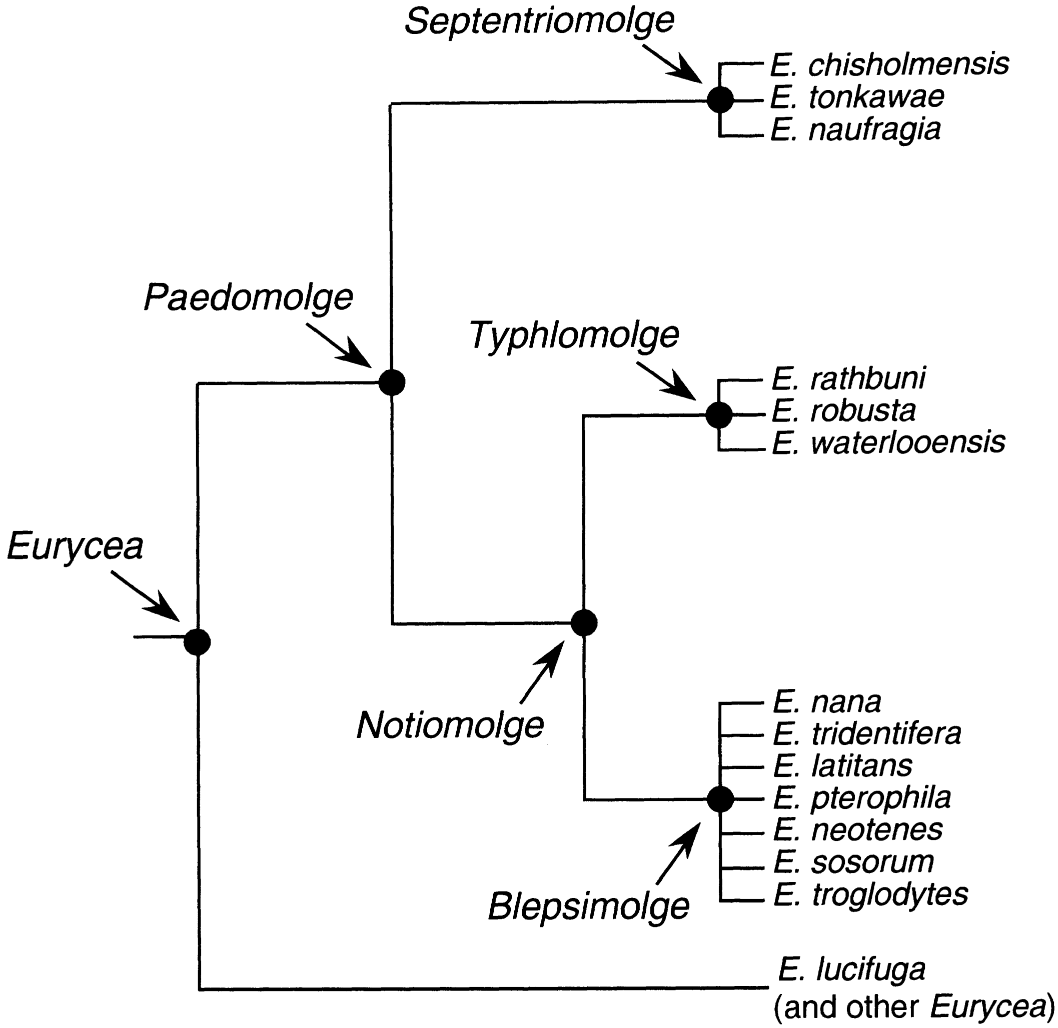

FIG. 5.—Nomenclature of the clades of central Texas *Eurycea*. The node-based clade names are defined in the text.

species in our analysis, *E. waterlooensis* is most closely related to *E. rathbuni*, and this grouping was supported in ≥98% of bootstrap replicates (both parsimony and maximum likelihood analyses). However, because we were unable to include *E. robusta* in our analysis, the relationships among *E. rathbuni, E. robusta,* and *E. waterlooensis* remain unclear.

Mitchell and Reddell (1965) proposed that *Typhlomolge rathbuni* (the type species of *Typhlomolge* by monotypy) be placed in the genus *Eurycea*. This taxonomic change was supported by the phylogenetic relationships inferred by Chippindale et al. (2000), because they found *T. rathbuni* to be more closely related to some species of *Eurycea* than all the species of *Eurycea* are to one another (see also Fig. 4). However, this change is required only because of the ranked nature of Linnaean nomenclature. The name *Typhlomolge* is still available for a monophyletic group within *Eurycea* (Fig. 5), regardless of the rank to which it is assigned. According to the rules of the International Code of Zoological Nomenclature (ICZN, 1999), any uninominal name of a "... genus-group division of a genus, even if it is proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as 'section' or 'division' . . ." (Art. 10.4). Therefore, if the name *Typhlomolge* is associated with a group within the genus *Eurycea,* then *Typhlomolge* is a subgenus under ICZN rules, even if more or less inclusive names are also proposed within *Eurycea.* A name for a more inclusive clade that includes *Typhlomolge* (but is still part of *Eurycea*) is also a subgenus under the ICZN rules (even though we may refer to it as a section or some other informal rank).

The name *Typhlomolge* could be applied to several different clades that include the type species (*E. rathbuni*). However, the characters that have been used to diagnose this group (e.g., by Potter and Sweet, 1981) indicate that the name *Typhlomolge* logically should be associated with the clade that contains *E. rathbuni, E. robusta,* and *E. waterlooensis* (Fig. 5). This group, however, is phylogenetically imbedded deep within *Eurycea.* Under the Code, the choice of one genus (for *Eurycea*) or several genera (for *Eurycea, Typhlomolge,* etc.) is subjective. If *Eurycea* is ranked as a genus and *Typhlomolge* as a subgenus, then the treatment of intermediate clades between *Eurycea* and *Typhlomolge* is somewhat problematic. Under the Code, these intermediate groups will also be subgenera (even if named as sections or divisions), thus creating subgenera within subgenera. A phylogenetic system of nomenclature that does not require ranks (e.g., de Queiroz and Gauthier 1990, 1992, 1994; see also http://www.ohiou.edu/phylocode/) would eliminate the subjective nature of ranking decisions, and would not create misleading ranks (e.g., subgenera that are imbedded within other subgenera). Under such a system, the name *Typhlomolge* would be used to refer to a distinctive monophyletic group of subterranean blind salamanders (Fig. 5), without reference to a particular subjective rank. The hierarchical relationships of this taxon to others could be depicted by other means, such as a phylogenetic tree or indenting conventions. Although we look forward to modifications of the rules of nomenclature to allow the use of unranked names, we here follow the rules of the ICZN in naming groups within *Eurycea.* However, we choose to define all clade names phylogenetically (in addition to the ICZN requirements of a diagnosis and type species designation) so that they may also be used under a phylogenetic system of nomenclature and will be clear in their phylogenetic meaning.

We here define *Typhlomolge* Stejneger 1896 as "the last common ancestor of *Eurycea rathbuni* (Stejneger 1896), *Eurycea robusta* (Potter and Sweet 1981), and *Eurycea waterlooensis* Hillis, Chamberlain, Wilcox, and Chippindale 2001, and all of the descendants of that common ancestor." We define *E. robusta* as part of this group, even though we have no sequence data for this species, on the basis of the morphological evidence described by Potter and Sweet (1981) in support of *Typhlomolge.* We include all three species in the definition for the clade *Typhlomolge,* because the relationships among the three species are not clear, and any two species potentially could define a clade that excludes the third species. The name *Typhlomolge* is formed from the Greek *typhlos,* meaning "blind," and the generic name *Molge* Merrem 1820 (a synonym of *Triturus* Rafinesque 1815), which in turn is derived from the German word *molch,* meaning salamander or monster (Stejneger, 1907). Because *molch,* and therefore *Typhlomolge,* is masculine, the original name *Typhlomolge robusta* was misformed, and should have been *Typhlomolge robustus.* However, the combination *Eurycea robusta* matches in gender, so no change is needed in the present combination under ICZN rules. The known content of *Typhlomolge* is limited to *E. rathbuni, E. robusta,* and *E. waterlooensis.* We also define *Eurycea* Rafinesque 1822 as "the last common ancestor of *Eurycea rathbuni* (Stejneger 1896) and *Eurycea lucifuga* Rafinesque 1822, and all of the descendants of that common ancestor." *Eurycea lucifuga* is the type species of *Eurycea.* Rafinesque (1822) suggested that the name *Eurycea* was mythological in origin, although the etymology is not clear.

Our inferred phylogenetic relationships of the central Texas paedomorphic spring and cave salamanders are largely consistent with results based on allozyme and DNA data presented by Chippindale et al. (2000), and these relationships are now well-enough understood that we name the following major clades within this group. Although all of these names are subgenera under ICZN rules, we use the informal terms "section" and "division" to indicate the relative hierarchy of the names for their use under Linnaean nomenclature. The species names of all the species in these groups can be treated identically under Linnaean nomenclature and phylogenetic nomenclature (Cantino et al., 1999) by treating *Eurycea* as a genus under the former system and as a recommended clade address for the species under the latter system. This is one version of Method M of Cantino et al. (1999) for naming species under a system of phylogenetic nomenclature.

Septentriomolge new clade (subgenus)

Definition.—The last common ancestor of *Eurycea tonkawae* Chippindale, Price, Wiens, and Hillis 2000, *Eurycea chisholmensis* Chippindale, Price, Wiens, and Hillis 2000, and *Eurycea naufragia* Chippindale, Price, Wiens, and Hillis 2000, and all of the descendants of that common ancestor.

Diagnosis.—The following combination of nucleotide states within the cytochrome *b* gene is diagnostic for *Septentriomolge.* The numbers refer to the positions within the aligned sequences referenced in Appendix I; position 1 corresponds to position 16268 of the complete *Xenopus laevis* mitochondrial genome (GenBank accession number M10217). These character states are fixed within and unique to *Septentriomolge* in our analysis: 13: G, 43: T, 58: T, 85:C, 91: C, 110: T, 119: C, 136: C, 160: T, 163: T, 166: C, 178: C, 248: C, 265: A, 271: A, 301: T, 309: T, 328: C, 424: C, 473: G, 552: T, 574: C, 614: C, 652: C, 660: T, 670: T, 688: G, 712: G, 721: T, 733: G, 736: G, 769: G, 778: A, 823: T, 865: C, 884: C, 890: C, 903: C, 922: C, 934: C, 940: T, 985: T, 1015: G, 1016: T, and 1018: T.

Type species.—*Eurycea chisholmensis.*

Content.—This clade is the "northern group" of Chippindale et al. (2000), and includes all the species of central Texas *Eurycea* from north of the Colorado River in Texas (currently, *E. tonkawae, E. chisholmensis,* and *E. naufragia*).

Etymology.—The name *Septentriomolge* is formed from the Latin word *septentrionalis,* meaning "northern," and the old generic name *Molge* (see the etymology of *Typhlomolge,* above). *Septentriomolge* is masculine in gender.

Blepsimolge new clade (subgenus)

Definition.—The last common ancestor of *Eurycea neotenes* Bishop and Wright 1937, *Eurycea nana* Bishop 1941, and *Eurycea troglodytes* Baker 1957, and all of the descendants of that common ancestor.

Diagnosis.—The following combination of nucleotide states within the cytochrome *b* gene is diagnostic for *Blepsimolge.* The numbers refer to the positions within the aligned sequences referenced in Appendix I; position 1 corresponds to position 16268 of the complete *Xenopus laevis* mitochondrial genome (GenBank accession number M10217). These character states are fixed within and unique to *Blepsimolge* in our analysis: 247: C, 514: G, 770: A, 805: C, 866: T, 891: C, 1021: C, and 1024: C.

Type species.—*Eurycea nana.*

Content.—This clade contains *E. latitans, E. nana, E. neotenes, E. sosorum, E. tridentifera, E. troglodytes,* and *E. pterophila.*

Etymology.—*Blepsimolge* is formed from the Greek word *blepsis* (meaning "seeing" or "sight") and the generic name *Molge* (see above). The names *Blepsimolge* and *Typhlomolge* refer to the respective sister clades of primarily sighted and blind paedomorphic salamanders in central Texas. *Blepsimolge* is masculine in gender.

Notiomolge new clade (division)

Definition.—The last common ancestor of *Eurycea rathbuni* (Stejneger 1896) and *Eurycea neotenes* Bishop and Wright

1937, and all of the descendants of that common ancestor.

Diagnosis.—The following combination of nucleotide states within the cytochrome *b* gene is diagnostic for *Notiomolge.* The numbers refer to the positions within the aligned sequences referenced in Appendix I; position 1 corresponds to position 16268 of the complete *Xenopus laevis* mitochondrial genome (GenBank accession number M10217). These character states are fixed within and unique to *Notiomolge* in our analysis: 4: C, 22: C, 79: C, 250: C, 319: T, 367: C, 403: C, 415: T, 427: T, 448: C, 545: A, 556: A, 577: C, 616: T, 619: T, 784: C, 826: T, 863: T, 904: T, 926: A, 943: C, 946: G, 973: C, 976: C, 982: A, and 1003: C.

Type species.—*Eurycea neotenes.*

Content.—This clade contains all the species of paedomorphic *Eurycea* in central Texas that occur south of the Colorado River. It includes all the species in the clades *Typhlomolge* and *Blepsimolge,* and is equivalent to the "southern group" of Chippindale et al. (2000).

Etymology.—*Notiomolge* is formed from the Greek word *notios* (meaning "southern") and the generic name *Molge* (see above), and is masculine in gender.

Paedomolge new clade (section)

Definition.—The last common ancestor of *Eurycea rathbuni* (Stejneger 1896) and *Eurycea tonkawae* Chippindale, Price, Wiens, and Hillis 2000, and all of the descendants of that common ancestor.

Diagnosis.—The following combination of nucleotide states within the cytochrome *b* gene is diagnostic for *Paedomolge.* The numbers refer to the positions within the aligned sequences referenced in Appendix I; position 1 corresponds to position 16268 of the complete *Xenopus laevis* mitochondrial genome (GenBank accession number M10217). These character states are fixed within and unique to *Paedomolge* in our analysis: 1:A, 10: C, 115: A, 118: T, 127: C, 133: T, 161: A, 187: C, 190: T, 196: T, 199: T, 244: A, 337: T, 341: T, 355: A, 400: A, 430: C, 431: T, 457: A, 466: T, 481: G, 496: C, 536: T, 541: A, 544: T, 553: A, 562: C, 565: C, 566: A, 571: C, 601: C, 628: A, 634: A, 658: T, 667: C, 668: C, 676: A, 680: A, 682: T, 692: A, 694: A, 700: A, 704: A, 706: A, 716: C, 742: A, 766: A, 856: A, 898: A, 902: A, 919: C, 929: T, 930: C, 931: A, 932: T, 941: A, 978: C, 980: C, 988: T, 991: T, and 1023:T.

Type species.—*Eurycea tonkawae.*

Content.—This clade contains all the spring and cave *Eurycea* of the Edwards Plateau of central Texas (see content of *Blepsimolge, Typhlomolge,* and *Septentriomolge*).

Etymology.—*Paedomolge* is formed from the Greek prefix *paedo-* (from the Greek word *paidos,* meaning "child") and the generic name *Molge* (see above). The name refers to the paedomorphic form of most of the species within this clade (a few naturally transforming populations are known within the *E. troglodytes* complex). *Paedomolge* is masculine in gender.

BIOGEOGRAPHY

Figure 4 indicates that the oldest split among the species of *Paedomolge* (the paedomorphic salamanders of the Edwards Plateau) was between the clade north of the Colorado River (*Septentriomolge*) and the clade south of the Colorado River (*Notiomolge*). This split presumably resulted from the action of the Colorado River as it cut down through the water-bearing strata of the Edwards Aquifer. The Edwards Plateau was first uplifted in the late Cretaceous, but the erosion of the river through the aquifer-bearing Edwards Limestone formation was completed during a later round of uplifting in the Miocene (Abbott, 1975; Ragsdale, 1960; Woodruff and Abbott, 1986). Today, there are believed to be few or no hydrological connections between the portions of the Edwards Aquifer north and south of the Colorado River (Slade et al., 1986). The species of *Septentriomolge* differ from the species of *Notiomolge* at an average of 180 of 1026 positions (17.5%) of the cytochrome *b* gene sequenced in this study (range: 167–194 differences, or 16.3–18.9%). Within *Notiomolge,* there is a primary split between *Typhlomolge* and *Blepsimolge,* which indicates a relatively ancient speciation event between the subterranean and the largely epigean species (with more recent colonization of subterranean habitats by *E. latitans, E. tridentifera,* and some populations of the other species of *Blepsimolge*). The average number of nucleotide changes between the species of *Typhlomolge* and *Blepsimolge* is 96 of 1026, or 9.4% (range: 84–102, or 8.2–10.0%). The level of sequence divergence between the two species of *Typhlomolge* at Barton Springs and San Marcos Springs (3.3% between *E. waterlooensis* and *E. rathbuni*) is similar to the level of sequence divergence between the two species of *Blepsimolge* at these localities (2.3% between *E. nana* and *E. sosorum*). A third pair of subterranean/surface species exists in the Blanco River drainage (*E. robusta* and *E. pterophila*). Therefore, the separation of these three segments of the Edwards Aquifer may have resulted in the co-speciation of one species of *Typhlomolge* and one species of *Blepsimolge* in each hydrologic area.

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APPENDIX I

Localities for Populations of Central Texas Eurycea *Examined for Cytochrome* b *Sequences*

All localities are in Texas unless otherwise noted. Specimen numbers and GenBank accession numbers are in parentheses following species names; museum acronyms follow Leviton et al. (1985).

Eurycea chisholmensis (TNHC 52770, GenBank AY014841): Bell Co., Salado Springs, 30° 56′ 37″ N, 97° 32′ 31″ W (type locality); *E. latitans* (TNHC 54536, GenBank AY014849): Kendall Co., Pfeiffer's Water Cave, 29° 45′ 44″ N, 98° 39′ 59″ W (subterranean extension of type locality); *E. m. multiplicata*: (TNHC 60315, GenBank AY014854): Polk Co., AR, Band's Spring at Forest Service camp approximately 40 km SE of Mena; *E. nana* (UTA A-53663, GenBank AY014846): Hays Co., San Marcos Springs, 29° 53′ 35″ N, 97° 55′ 50″ W (type locality); *E. naufragia* (TNHC 51005, GenBank AY014843): Williamson Co., Cedar Breaks Hiking Trail Spring, 30° 39′ 36″ N, 97° 45′ 02″ W; *E. neotenes*: (TNHC 60313, GenBank AY014850): Bexar Co., Helotes Creek Spring, 29° 38′ 15″ N, 98° 41′ 40″ W (type locality); *E. pterophila* (TNHC 60316, GenBank AY014851): Hays Co., Fern Bank Springs, 29° 59′ 00″ N, 98° 00′ 49″ W (type locality); *E. rathbuni*: (TNHC 51174, GenBank AY014844; TNHC 60314, GenBank AY014845): Hays Co., Rattlesnake Cave, 29° 54′ 07″ N, 97° 55′ 17″ W; *E. sosorum* (TNHC 50919, GenBank AY014857): Travis Co., Barton Springs, 30° 15′ 49″ N, 97° 46′ 14″ W (type locality); *E. tonkawae* (TNHC 60311, GenBank AY014842): Travis Co., Stillhouse Hollow Springs, 30° 22′ 28″ N, 97° 45′ 55″ W (type locality); *E. tridentifera* (TNHC 51057, GenBank AY014848): Comal Co., Honey Creek Cave, 29° 50′ 50″ N, 98° 29′ 30″ W (type locality); *E. troglodytes* (TNHC 60312, GenBank AY014853): Bandera Co., Sutherland Hollow Spring, 29° 44′ 58″ N, 99° 25′ 36″ W; (TNHC 60318, GenBank AY014852): Gillespie Co., Trough Spring, 30° 08′ 36″ N, 99° 04′ 40″ W; *E. waterlooensis* (TNHC 60201, GenBank AY014855): Travis Co., Sunken Gardens Spring (type locality; holotype); (THNC 60203, GenBank AY014856): Travis Co., Barton Springs Pool (paratype), 30° 15′ 49″ N, 97° 46′ 14″ W; *E.* sp. (Pedernales) (TNHC 60317, GenBank AY014847): Travis Co., Hammett's Crossing Spring, 30° 20′ 28″ N, 98° 08′ 14″ W.