
DISTRIBUTION AND RELATIVE ABUNDANCE OF TENNESSEE CAVE SALAMANDERS (*GYRINOPHILUS PALLEUCUS* AND *GYRINOPHILUS GULOLINEATUS*) WITH AN EMPHASIS ON TENNESSEE POPULATIONS

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Abstract.—The Tennessee Cave Salamander complex (*Gyrinophilus palleucus* and *G. gulolineatus*) consists of three obligate cave-dwelling taxa inhabiting subterranean waters of east and central Tennessee, north Alabama, and northwest Georgia. Although ranges of these taxa are poorly understood, their populations are reportedly small and declining. The IUCN lists *G. gulolineatus* as "Endangered" and *G. p. necturoides* as "Vulnerable"; whereas, NatureServe lists *G. gulolineatus* (G1) and *G. p. necturoides* (G2G3T1) as Critically Imperiled. To better determine the distribution and relative abundance of extant populations, we searched 113 cave streams in middle and east Tennessee, seven in northwest Georgia, 13 in north Alabama and two in southern Kentucky. We found 1183 salamanders, including 63 *G. gulolineatus*, 681 *G. palleucus*, and 439 *G. porphyriticus* (Spring Salamanders), during 229 surveys of 135 caves. *Gyrinophilus palleucus* and *G. gulolineatus* were observed in more caves (30) than *G. porphyriticus* (17 caves). Members of the complex were found at 52% (12 of 23) of historic caves and at 16% (18 of 110) of non-historic caves. We extended the known distribution of *G. palleucus* in the Collins, Elk, Duck, and lower Tennessee River watersheds of central Tennessee, and the distribution of *G. gulolineatus* into the Clinch River watershed of east Tennessee. We found robust populations at historic sites thought to be declining; therefore, our data do not support previous claims of range-wide declines. However, the fragile ecosystems of subterranean environments make populations vulnerable to habitat alteration. In particular, Knox Co. populations of *G. gulolineatus* and Rutherford and Wilson cos. populations of *G. palleucus* are located in areas of rampant urban development associated with significant surface habitat and concomitant groundwater alteration.

Key Words.—Cumberland Plateau; *Gyrinophilus gulolineatus*; *Gyrinophilus palleucus*; Middle Tennessee; Tennessee Cave Salamanders; threats

INTRODUCTION

The Tennessee Cave Salamander complex comprises populations of paedomorphic salamanders that inhabit subterranean waters of middle and east Tennessee, northwest Georgia, and north Alabama (Fig. 1; Beachy 2005a,b; Redmond and Scott 1996; Petranka 1998). Based on morphology, three taxa are recognized within the complex (Brandon 1966, 1967a). The Pale Salamander (*Gyrinophilus palleucus palleucus*, Fig. 2) is associated with caves in the Crow Creek drainage system of the Lower Tennessee River watershed of Franklin Co., Tennessee, and Jackson Co., Alabama. The Big Mouth Cave Salamander (*G. p. necturoides*, Fig. 3A) is known from one cave in the upper Elk River watershed in the Eastern Highland Rim of Grundy Co., Tennessee. The Berry Cave Salamander (*G. gulolineatus*, Fig. 4) is associated with caves of the Valley and Ridge physiographic province of east Tennessee. Populations discovered outside the described ranges of recognized taxa (e.g., northwest Georgia, Cooper 1968; Collins River watershed, Miller 1995; Duck River watershed, Samoray and Garland 2002) are generally identified simply as *G. palleucus*. Therefore,

the systematics and genetic relationships of populations comprising the recognized taxa are unknown, their distributions are poorly understood, and the ranks assigned are controversial (Collins 1991; Petranka 1998; Duellman and Sweet 1999; Crother et al. 2000; Beachy 2005a,b).

Populations of *G. palleucus* and *G. gulolineatus* are putatively small, mainly because few salamanders are found during cave surveys (Caldwell, R.S., and J.E. Copeland. 1992. Status and habitat of the Tennessee Cave Salamander, *Gyrinophilus palleucus*. Unpublished report, Tennessee Wildlife Resources Agency, Nashville, Tennessee, USA.; Petranka 1998; Beachy 2005a,b). Because of the suspected small population sizes, limited geographic distribution, and subterranean habitats, *G. palleucus* and *G. gulolineatus* are thought to be particularly vulnerable to habitat degradation caused by agricultural and silvicultural practices, urbanization, and over-collecting (Simmons 1975; Caldwell and Copeland 1992. *op. cit.*; Petranka 1998; Beachy 2005a,b). Particular concern has been expressed for the Knox County populations of *G. gulolineatus* and for *G. p. necturoides*. Populations of the former presumably are adversely affected by expanding metropolitan

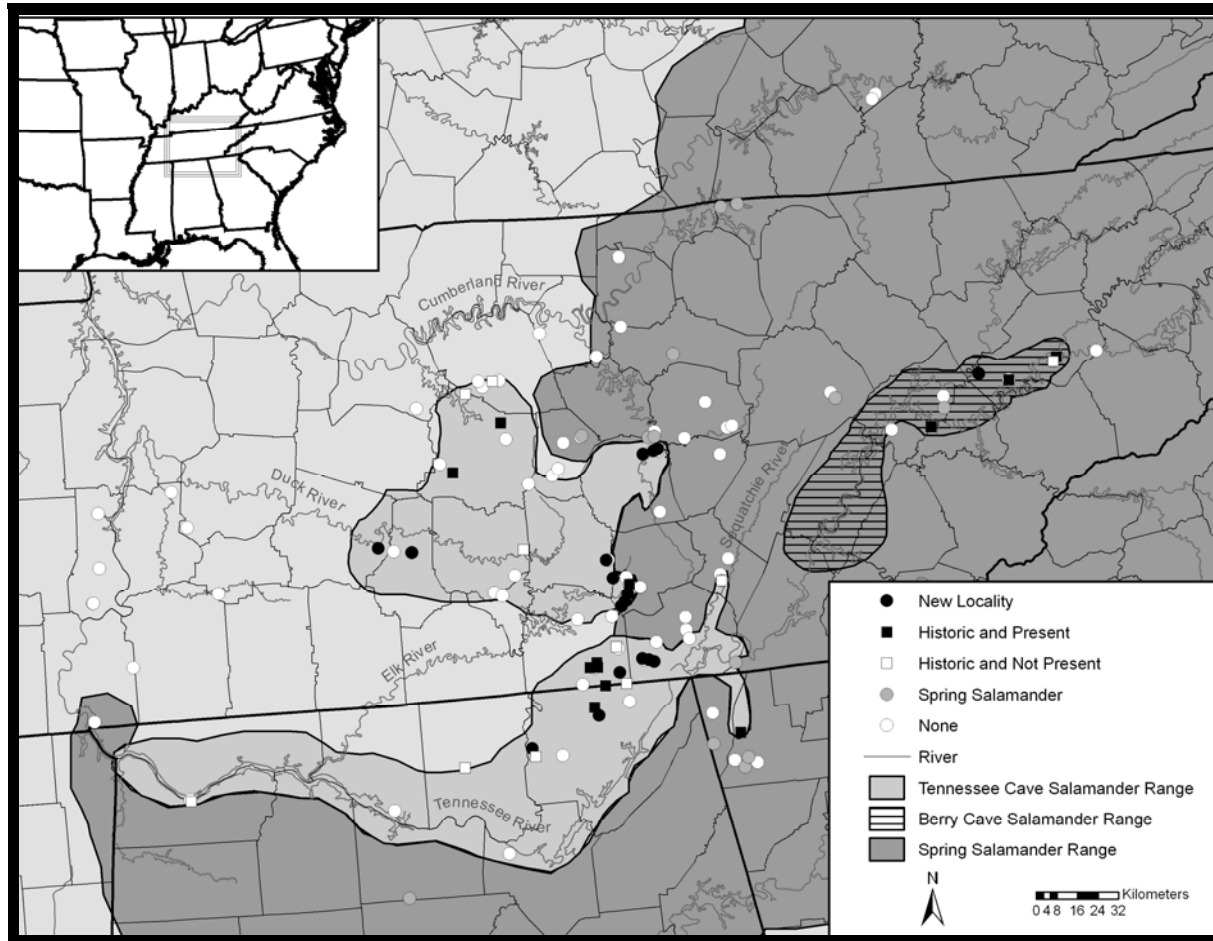


FIGURE 1. Distribution of sampling localities and occurrence records for subterranean *Gyrinophilus* observed during the study. Black symbols indicate localities with Tennessee Cave Salamander complex observations.

Knoxville, while the latter is vulnerable because it is known from a single cave (Simmons 1975; Caldwell and Copeland 1992 *op. cit.*). NatureServe (NatureServe. 2006. NatureServe Explorer: An online encyclopedia of life. Version 6.0. Available from <http://www.natureserve.org/explorer>. [Accessed 26 October 2006]) lists *G. gulolineatus* (G1) and *G. p. necturoides* (G2G3T1) as "Critically Imperiled"; whereas, the IUCN lists *G. gulolineatus* as "Endangered" and *G. p. necturoides* as "Vulnerable" (IUCN 2004. *Gyrinophilus gulolineatus*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. Available from www.iucnredlist.org. [Accessed 07 January 2008]; IUCN 2004. *Gyrinophilus palleucus*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. Available from www.iucnredlist.org [Accessed 07 January 2008].). However, the United States Fish and Wildlife Service currently does not assign special protection designation to any member of the complex. The Tennessee Wildlife Resources Agency does not recognize the Berry Cave Salamander as a distinct species and does not consider

subspecific designations when determining conservation status; consequently, all members of the complex share the same state "Threatened" status (Withers et al. 2004). *Gyrinophilus palleucus* is listed as a species of special concern in Georgia (Georgia Department of Natural Resources 2004) and as a protected species in Alabama (Godwin, J.C. 2000. Reassessment of the historical and search for new localities of the Tennessee Cave Salamander (*Gyrinophilus palleucus*) in Alabama. Alabama Natural Heritage Program. Unpublished report. Alabama Department of Conservation and Natural Resources, Montgomery, Alabama, USA.). Because of the concern of declining populations and limited geographic distribution, we undertook this study to determine the status (extant or extirpated) and relative abundance (based on census data) of *G. palleucus* and *G. gulolineatus* in caves with historic records of occurrence. A second objective was to better define the distribution of the complex by searching caves lacking historic records.

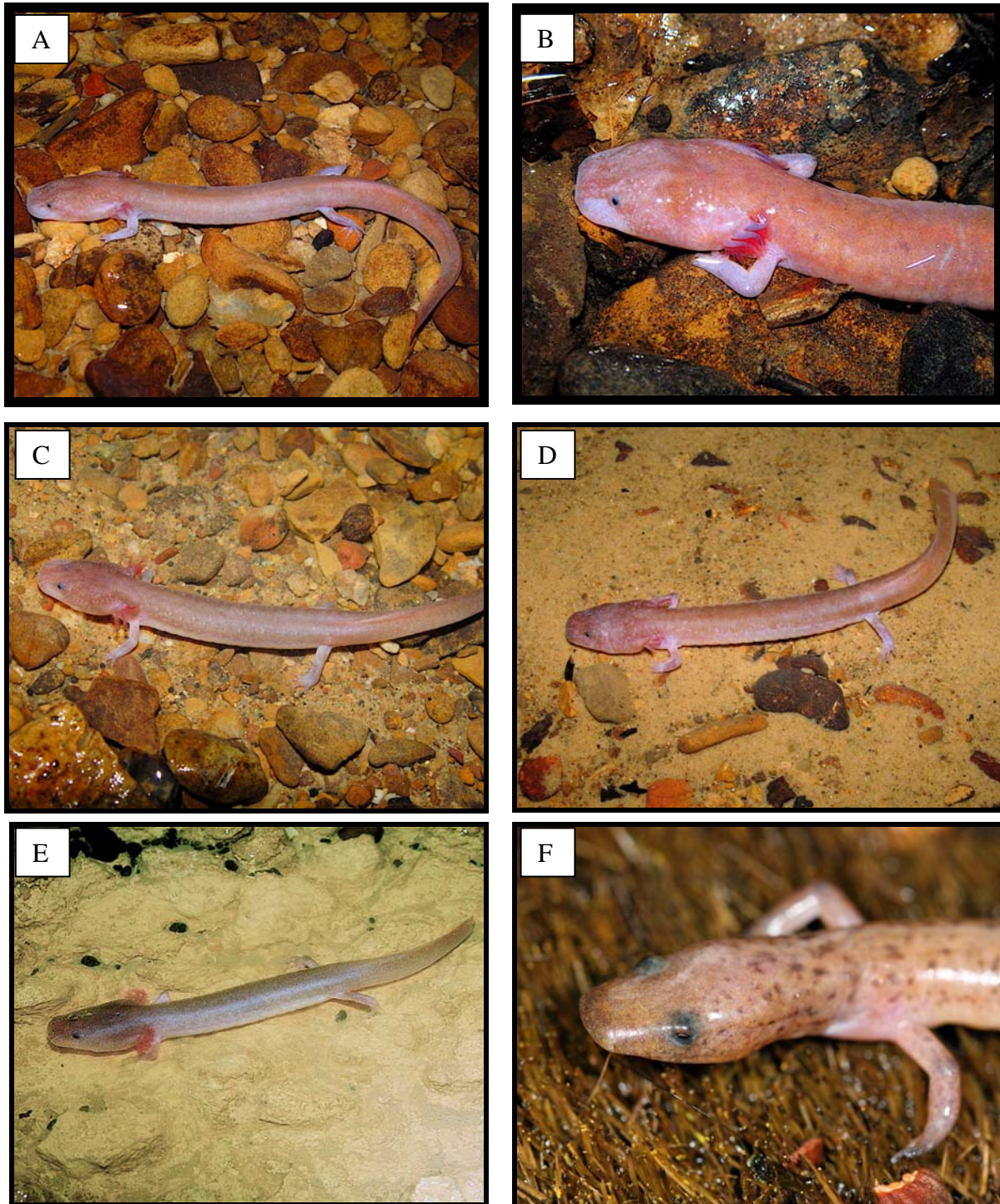


FIGURE 2. Photographs of the Pale Salamander (*G. palleucus palleucus*): A) Custard Hollow Cave, Franklin Co., Tennessee; B) Cave Cove Cave, Franklin Co., Tennessee; C) Shakerag Cave, Marion Co., Tennessee; D) Bluff River Cave, Jackson Co., Alabama; E) Jess Elliot Cave, Jackson Co., Alabama; and F) metamorphosed individual from Jess Elliot Cave, Jackson Co., Alabama.

METHODS

We searched for Tennessee Cave Salamanders (*G. p. palleucus*, *G. p. necturoides*, and *G. gulolineatus*) from

May 2004 through June 2007 in 113 cave streams in middle and east Tennessee, seven in northwest Georgia, 13 in north Alabama and two in southern Kentucky (Fig. 1). Tennessee Cave Salamanders have been documented

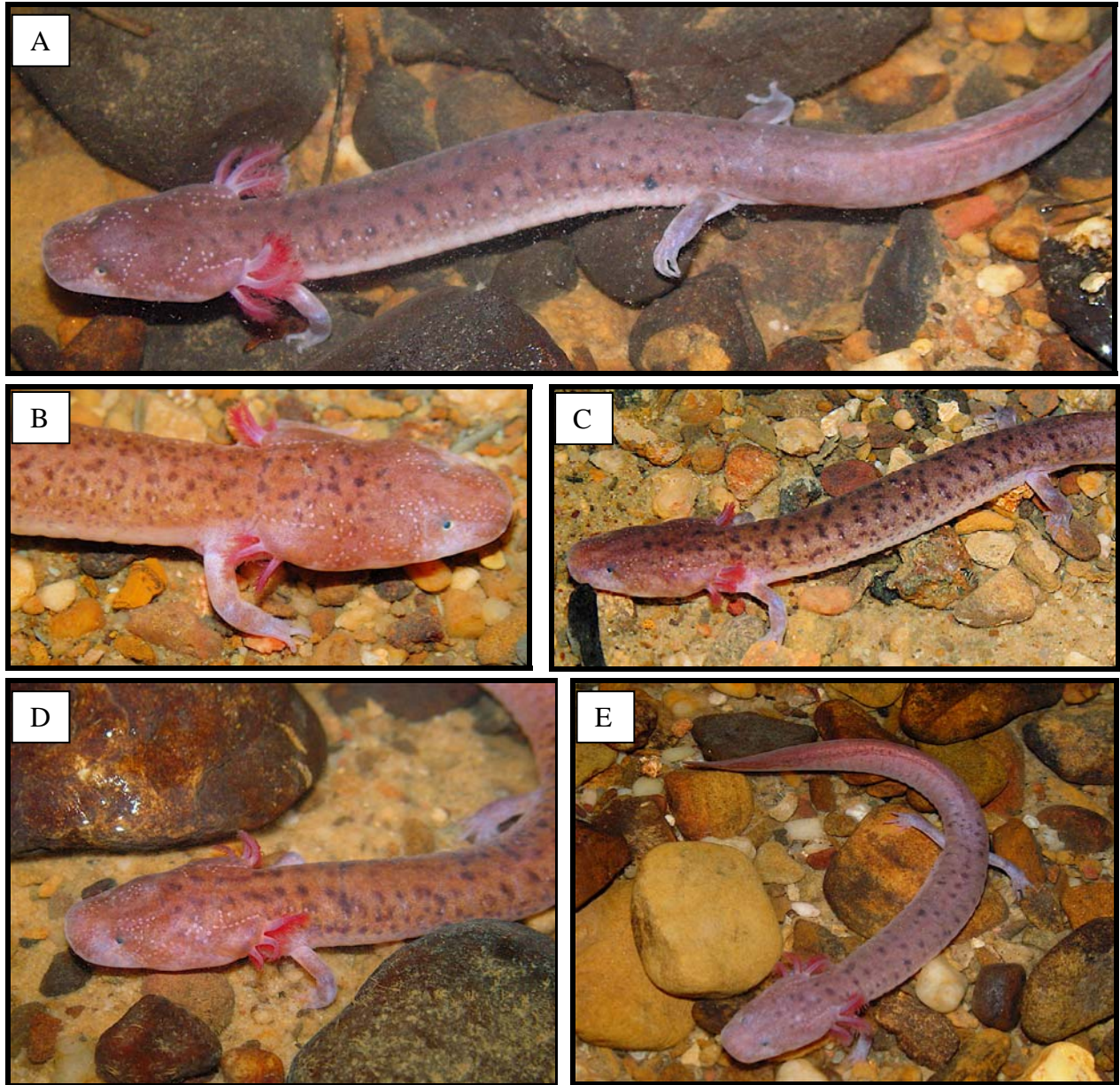


FIGURE 3. Photographs of the Big Mouth Cave Salamander (*G. palleucus necturoides*) from the Elk River watershed: A) Big Mouth Cave, Grundy Co., Tennessee; B) Smith Hollow Cave, Grundy Co., Tennessee; C) Crystal Cave, Grundy Co., Tennessee; D) Blowing Springs Cave, Coffee Co., Tennessee; and E) Lusk Cave, Coffee Co., Tennessee.

with voucher specimens, photographs or reliable sightings from 18 of these caves in Tennessee, five in Alabama, and one cave in Georgia (Appendix); these caves are hereafter referred to as historic localities. Note that two of these caves, Salt River Cave and Ranie Willis Cave, have entrances in Alabama as well as in Tennessee and often are included in lists of Alabama caves inhabited by *G. palleucus*. We conducted surveys during every month of the year, but concentrated searches during periods of favorable stream conditions (i.e., shallow, clear water with little flow). To locate

salamanders, we donned wetsuits and slowly walked along, waded through, or crawled in the cave stream channel and thoroughly scanned the streambed with the beams of our headlamps. We also carefully lifted flat rocks, small cobble, and detritus under which salamanders might seek refuge. Lifted rocks were returned to their original positions to minimize habitat disturbance. A tally of each individual found was kept, and a concerted effort was made to capture, with small bait nets, each salamander encountered. Captured salamanders were placed in clear plastic bags until their

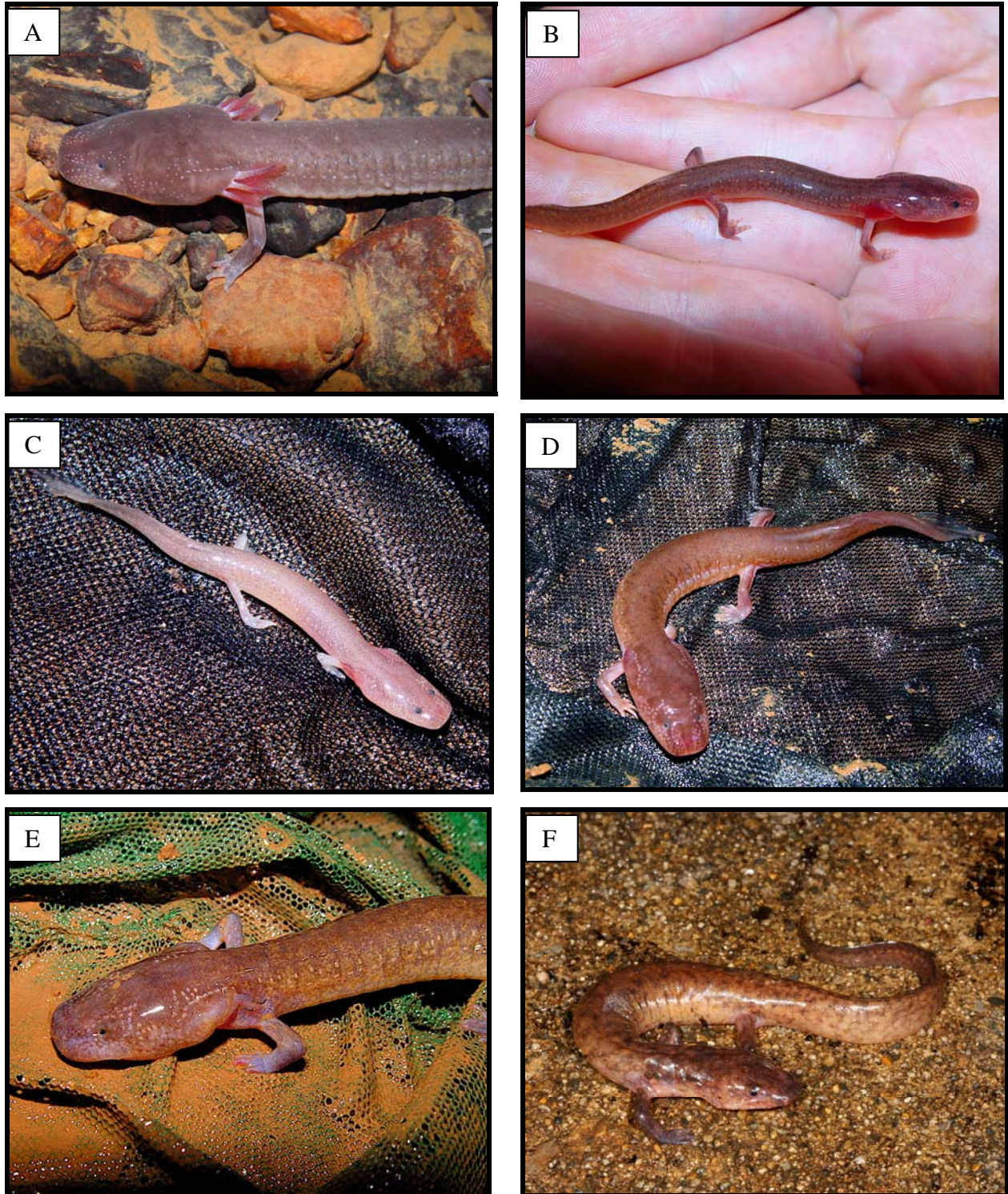


FIGURE 4. Photographs of the Berry Cave Salamander (*G. gulolineatus*) from the Upper Tennessee River watershed: A) Berry Cave, Roane Co., Tennessee; and B) Mudflats Cave, Knox Co., Tennessee. Berry Cave Salamanders from the Clinch River watershed in Knox Co., Tennessee: C) Aycock Spring Cave; D) Christian Cave. Larviform (E) and metamorphosed (F) adults from Meade Quarry Cave, Knox Co., Tennessee.

mass was determined to the nearest g with a small Pesola spring scale, and their total length (TL) and snout-vent length (SVL) were measured to the nearest mm using a small metric rule. Each captured salamander was classified as immature (< 70 mm SVL), or mature (> 70 mm SVL). All salamanders > 70 mm examined by

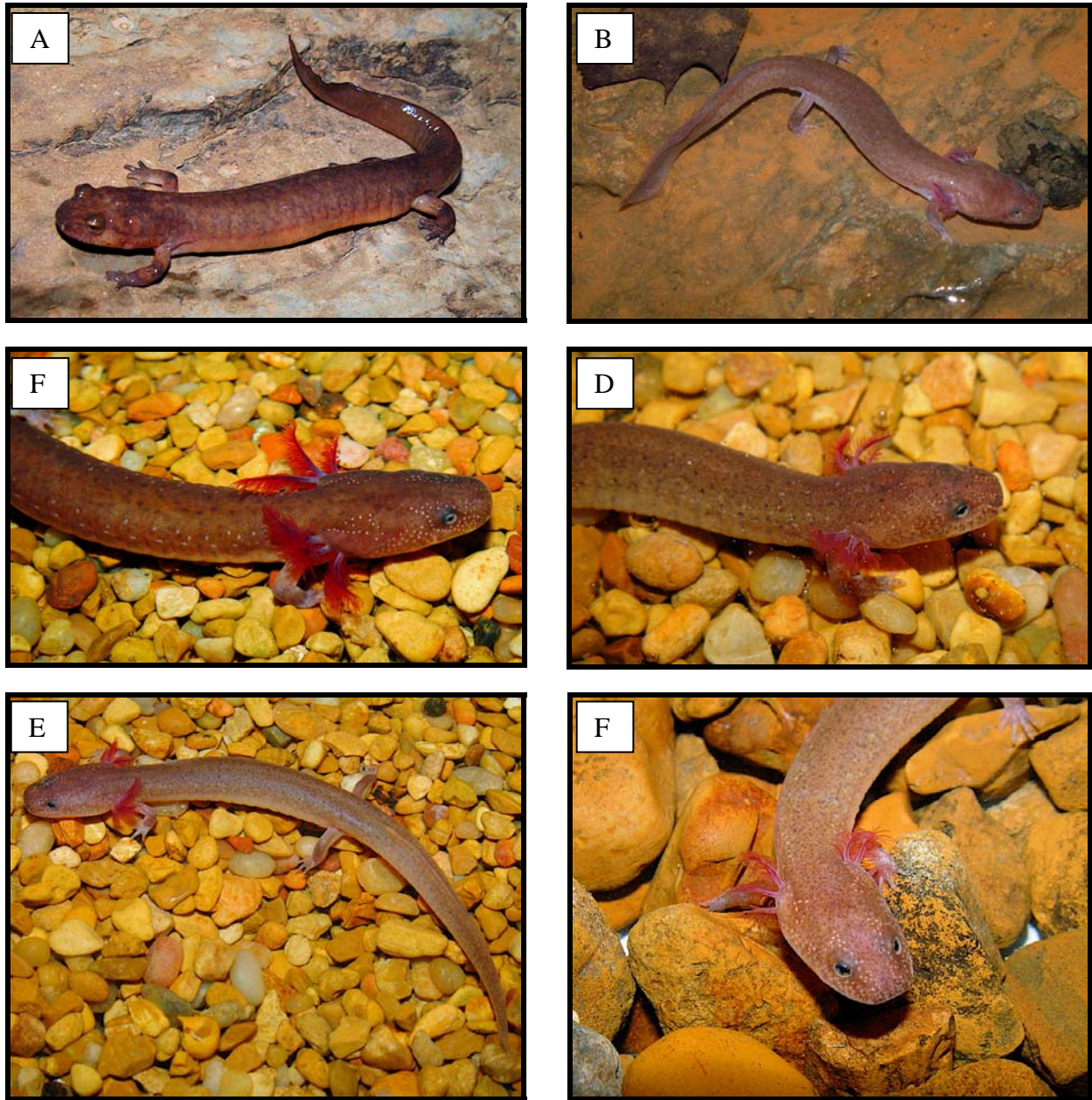


FIGURE 5. Photographs of Spring Salamanders (*G. porphyriticus*): A) adult from Cruze Cave, Knox Co., Tennessee; B) larva from Cruze Cave, Knox Co., Tennessee; C) Stone Cave, Sequatchie Co., Tennessee; D) Gunters Cave, Cannon Co., Tennessee; E) Gar Island Cave, DeKalb Co., Tennessee; and F) Pauley Cave, DeKalb Co., Tennessee.

Simmons (1975) were considered sexually mature, although some males as small as 66 mm SVL may be mature. Additionally, we excised the tail tip from one or more salamanders captured at each cave for subsequent genetic analyses.

The closely related Spring Salamander, *G. porphyriticus*, also inhabits caves in middle and east Tennessee, northwest Georgia, and north Alabama (Petranka 1998; Beachy 2005c). Although larval *G. porphyriticus* are distinguished from Tennessee Cave

Salamanders by a suite of morphological features (Brandon 1966), we used presence of a discernable iris and relative eye size to distinguish *G. porphyriticus* from *G. pallidus* and *G. gulolineatus* in the field. These characters have been used to identify newly discovered populations in the Central Basin and Highland Rim: populations of salamanders with small eyes lacking a visible iris were identified as *G. pallidus* (Miller and Walther 1994; Miller 1995; Samoray and Garland 2002), and populations of salamanders with large eyes and a

clearly visible iris were identified as *G. porphyriticus* (Niemiller 2004). Exceptionally, a population of salamanders with relatively large eyes and a visible iris found in the Sequatchie River Valley (Stone Cave) was identified as *G. palleucus* (Hollingsworth, K., D.E. Collins, and G.W. Benz. 1997. Tennessee Cave Salamander, *Gyrinophilus palleucus* survey – Greater Chattanooga Area, Tennessee. Unpublished Report. Tennessee Wildlife Resources Agency, Nashville, Tennessee, USA.).

RESULTS

We found 1183 individuals of *Gyrinophilus* during 229 surveys of 135 caves in Tennessee, Alabama, Georgia, and Kentucky (63 *G. gulolineatus*, 681 *G. palleucus*, and 439 *G. porphyriticus*; Appendix). Tennessee Cave Salamanders (*G. p. palleucus*, *G. p. necturoides*, and *G. gulolineatus*) were observed in more caves (30) than *G. porphyriticus* (17 caves). We identified *G. palleucus* or *G. gulolineatus* in 52% (12 of 23) of historic localities. We identified, based on

relative eye size and iris presence, salamanders in two historic localities, Cruze and Stone caves, as *G. porphyriticus*. Tennessee Cave Salamanders were observed in 16% (18 of 110) of non-historic sites (Appendix).

Historic Localities.—The number of salamanders found varied substantially among historic localities. For example, we found six or fewer salamanders per survey at Salt River, Snail Shell, Herring, Berry, Mudflats, Stone, and Fricks caves, but > 20 salamanders per survey at Sinking Cove, Cave Cove, Custard Hollow, Jess Elliot, Big Mouth, and Cruze caves (Appendix). Many of the salamanders found in Cruze Cave were metamorphosed (23%; Fig. 5A), the eyes of larviform individuals were noticeably larger than those inhabiting other Knox Co. caves, and the iris was clearly visible (Fig. 5B). Similarly, the iris was clearly visible in salamanders found at Stone Cave (Fig. 5C). The historic occurrence of *G. palleucus* at Stone Cave is based on the observation of three salamanders (two were collected) active at night in a small pool outside of the entrance

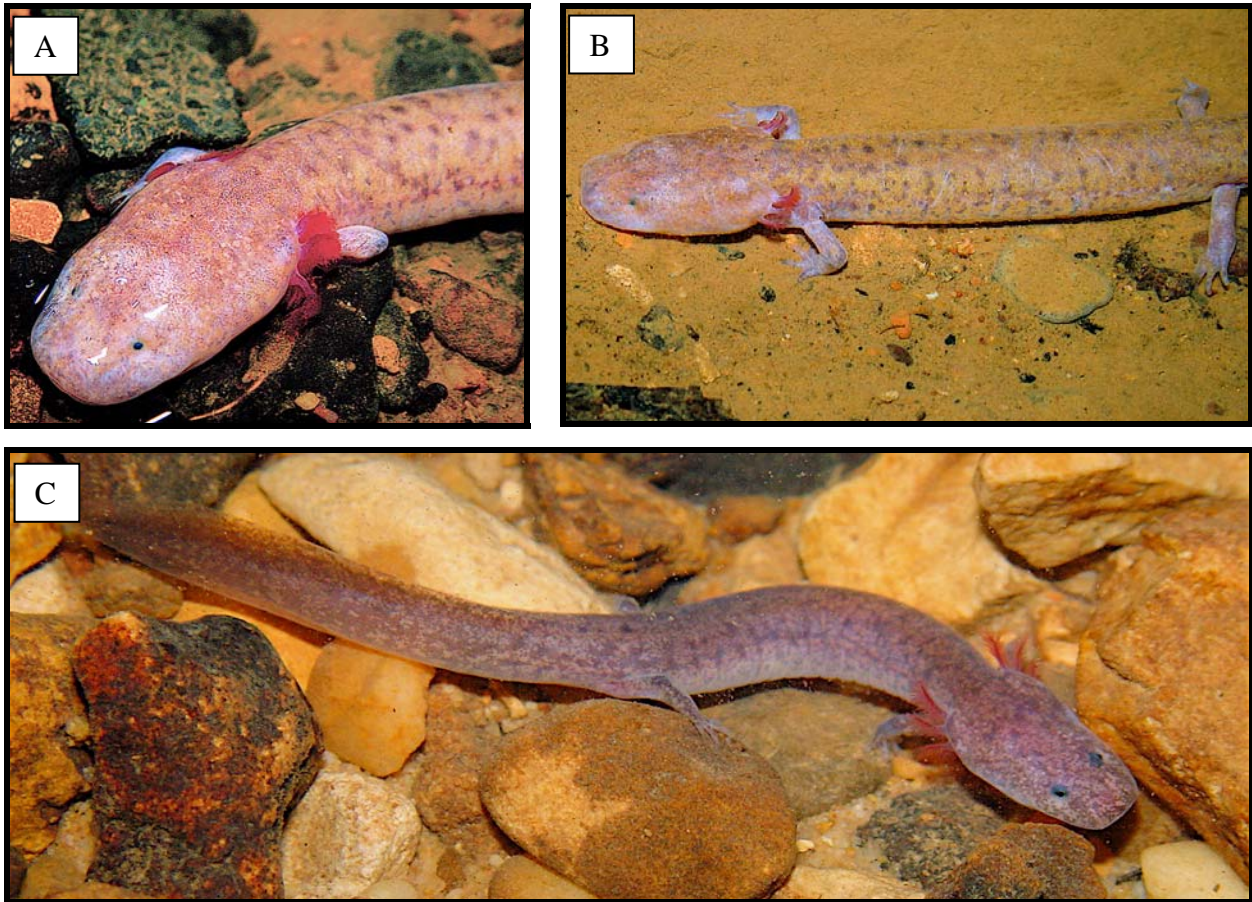


FIGURE 6. Tennessee Cave Salamanders from the Collins River watershed in Warren Co., Tennessee: A) Jaco Spring Cave; B) King Cave; and C) Sugarcookie Cave.

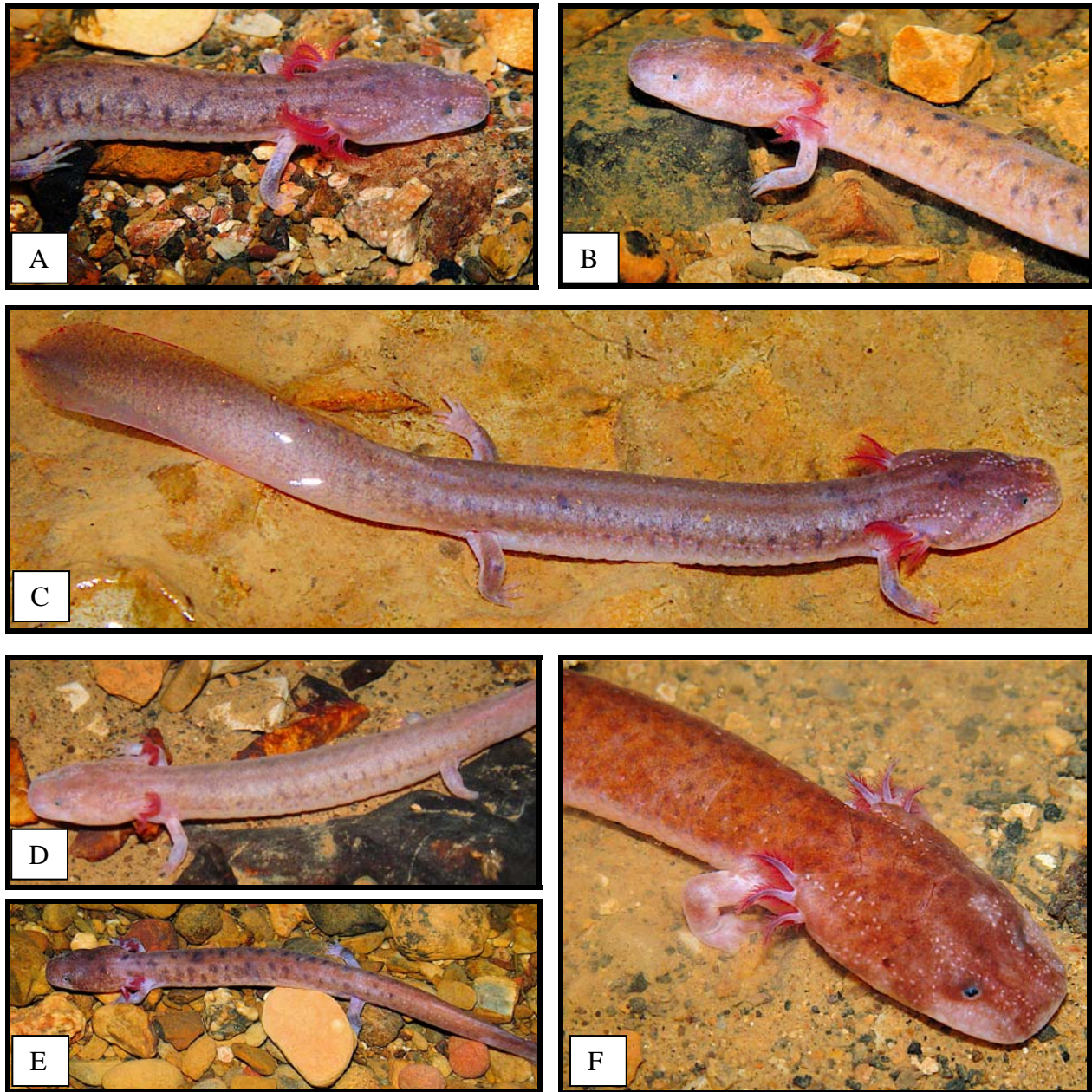


FIGURE 7. Tennessee Cave Salamanders from the Stones River watershed in Rutherford Co., Tennessee. A) Snail Shell Cave; B) Herring Cave; from the Duck River watershed: C) Pompie Cave, Maury Co., Tennessee; D) Gallagher Cave, Marshall Co., Tennessee; and from the Tennessee River watershed: E); and F) Gourneck Cave, Marion Co., Tennessee.

(Hollingsworth et al. 1997 *op. cit.*). All were larviform, but one of the collected salamanders underwent metamorphosis shortly after capture. Photographs of Stone Cave *Gyrinophilus* provided by Hollingsworth et al. (2007 *op. cit.*) clearly depict the iris in the relatively large eyes. The individuals we collected from this locality were nearly indistinguishable from the salamander shown in their report. Pending genetic analyses, we tentatively identified the Stone Cave population as *G. porphyriticus*. Nineteen larviform and

two metamorphosed *G. palleucus* were found in Jess Elliot Cave (Fig. 2E-F), and 33 larviform and three metamorphosed *G. gulolineatus* were found in Meade Quarry Cave (Fig. 4E-F).

We did not find *G. palleucus* at Buggytop, Fifth Entrance, Jackson, McFarland, McKinney Pit, Pattons, Ranie Willis, Shelta, or Yell caves (Appendix). Fifth Entrance, McFarland, McKinney Pit, Ranie Willis, Shelta, and Yell caves were surveyed only once, but Jackson, Pattons and Buggytop caves were searched 13,

7, and 2 times respectively (Appendix).

New Localities: Elk River Watershed.—We found *G. palleucus* in five of the 14 non-historic sites surveyed in this watershed. Each of these caves was located at base level along the Cumberland Plateau escarpment. Three caves, Crystal, Smith Hollow, and Trussell, were located in western Grundy Co., and two, Lusk and Blowing Spring, were located in eastern Coffee Co. We found few salamanders in Crystal, Lusk, Smith Hollow, and Trussell caves, but by comparison many salamanders in Blowing Spring Cave (Appendix). The subadult observed in Trussell Cave evaded capture. Adults had small eyes lacking a visible iris and the dorsum was heavily pigmented and spotted; however, ground color and dorsal spot size were variable (Fig. 3B-E). In comparison, juveniles were pale and lacked the dorsal spotting of adults. Tentatively, we identified all Elk River watershed populations as *G. p. necturoides*; however, genetic analyses are required to determine how closely related the six Elk River watershed populations are to each other, and to determine the relatedness of *G. p. necturoides* to other taxa within the complex.

Collins River Watershed.—We found *G. palleucus* inhabiting three of the ten caves surveyed in this region, all located along the banks of the Collins River north of McMinnville in Warren County (Appendix; Jaco Spring, Sugarcookie, and King). Previously, *G. palleucus* was known within this watershed only from an unnamed spring flowing into the Collins River near the Hwy 27 crossing at the base of Cardwell Mountain (Miller 1995). Thus, these new records extended the known distribution ca 11.5 aerial km northward, or 41 km down the Collins River to near its confluence with the Caney Fork River (currently inundated as a reservoir, Great Falls Lake). Few salamanders were observed in these caves (Appendix). Adults had exceptionally small eyes lacking a visible iris and the dorsum was light yellow-brown with scattered darker brown to black, irregularly shaped spots (Fig. 6A-B). In comparison, juveniles were pale and lacked the dorsal spotting of adults (Fig. 6C).

Upper Tennessee River Watershed/Upper Clinch River Watershed.—We found *G. gulolineatus* in two of the nine non-historic sites surveyed in this region. These caves were located in Hardin Valley, within the Clinch River watershed on opposite sides of Conner Creek in Knox Co. Only one individual was captured in each cave: a small and pale larva was captured in Aycock Spring Cave (Fig. 4C) and a heavily pigmented, relatively large larviform individual was captured 290 m to the southwest in Christian Cave (Fig. 4D). These records extended the known distribution into the Clinch River watershed and suggest that this species may be

associated with other minor stream systems in Knox and neighboring counties.

Lower Tennessee River Watershed.—We found *G. palleucus* in six of the 31 non-historic sites searched in this region. Three of the caves, Gourdneck, Lost Pig, and Shakerag, were located in the Guntersville Reservoir section of the Tennessee River watershed in Marion Co., Tennessee (Appendix). Few salamanders were observed in each of these caves (maximum of four observed in Lost Pig Cave) and we suspect that few individuals inhabited them. The coloration of the individuals found in Lost Pig Cave and Shakerag Cave was similar to that of *G. p. palleucus* (dorsum pale beige and lacking prominent spotting, Fig. 2C). In contrast, the coloration of the individual captured in nearby Gourdneck Cave resembled *G. p. necturoides* (darker dorsum flecked with small black spots, Fig. 7F). We also found *G. palleucus* in Garner Spring Cave, in southern Franklin Co., Tennessee (Appendix). Although we found two individuals in this cave, we did not capture either. Within Alabama, *G. palleucus* was observed in two non-historic localities, Bluff River Cave and Tony Sinks Cave in Jackson Co. Adults from Bluff River Cave resemble *G. p. palleucus* (Fig. 2D); however, adults from Tony Sinks Cave were spotted on a pale dorsum (Fig. 7E). Both caves support sizable populations.

Duck River Watershed.—We found *G. palleucus* in two of the six non-historic sites surveyed in this watershed (Gallagher Cave in Marshall Co., Pompey Cave in Maury Co.; Appendix) and thereby extended the known distribution ca 57 km westward (downstream) into the Central Basin within the Duck River watershed. We found few salamanders in these caves (Appendix). Adults from this region had small eyes lacking an iris and a spotted dorsum (Fig. 7C-D). The association of the Duck River watershed populations to other Central Basin populations and to recognized taxa is unknown, but under investigation.

Spring Salamanders (Gyrinophilus porphyriticus).—We found Spring Salamanders in 17 caves (Appendix), seven within the Cumberland Plateau (Anderson Spring, Gunters, Hurricane, Lacon Exit, Pigeon, Raccoon Mountain, and Spencer Rock), six within the Eastern Highland Rim (Gar Island, Pauley, Marcus, Mark Us, Ringing Rock River, and West Cemetery), one within the Sequatchie Valley (Stone, see above), and three within the Valley and Ridge (Cave Creek, Cruze, and Meades River, but see discussion on Cruze Cave above). Relatively few individuals were found in any cave within this region. We found only larval *G. porphyriticus* in most caves (Fig. 5D-F), with the exception of Anderson Spring, Cruze, and Raccoon

Mountain caves where several metamorphosed adults were observed.

DISCUSSION

Tennessee Cave Salamanders have been verified (either presently or historically) from more than 40 localities associated with the Interior Low Plateau and southern Cumberland Plateau of middle Tennessee (Caldwell and Copeland 1992 *op. cit.*; Redmond and Scott 1996; this study), north Alabama (Cooper 1968; Mount 1975; Godwin 2000 *op. cit.*), and northwest Georgia (Cooper 1968; Buhlmann and Wynn 1996; Buhlmann 2001). Localities associated with the southern Cumberland Plateau represent caves developed within stratified Mississippian-age limestone along both the eastern and western escarpments; whereas, caves along the escarpment of the Eastern Highland Rim and Central Basin are developed in older Ordovician limestone exposed as a result of the erosion of the Nashville Dome (Miller 1974). Additionally, caves along the Collins River in Warren Co. and within the Eastern Highland Rim are developed in the Mississippian Warsaw Limestone. Cave development along the western escarpment of the Cumberland Plateau and the Eastern Highland Rim presumably are occurring under similar conditions as both continue to retreat toward the southeast away from the Nashville Dome (Crawford 1987). Almost all caves systems inhabited by Tennessee Cave Salamanders along the escarpments of the Cumberland Plateau possess resurging streams and are developed near base level within the St. Louis, Monteagle, or Bangor Limestone at elevations ranging from 200 – 350 m depending upon local stratigraphy; an exception is Cave Cove Cave, which at 350 m is developed within the upper Bangor Limestone and contains a sinking stream. Additionally, cave systems developed along the escarpment are confined to the Eastern Highland Rim aquifer system (Brahana and Bradley 1986b) and are separated from the underlying Central Basin aquifer system by the Chattanooga Shale that effectively restricts vertical movement of water between the two aquifers.

Within the Eastern Highland Rim of Tennessee, *G. palleucus* inhabits two distinct regions: along the escarpment marking the transition into the Central Basin in the Duck River watershed in Bedford Co., and within the Collins River watershed in Warren Co. The single record from the escarpment is from a privately-owned cave (Samoray and Garland 2002) developed within the Ordovician Bigby-Cannon Limestone and contained within the Central Basin aquifer system (Brahana and Bradley 1986a); whereas, localities along the Collins River are developed within the Mississippian Warsaw Limestone both at and slightly above (10-20 m) present-day river level and contained within the Eastern

Highland Rim aquifer system (Brahana and Bradley 1986b).

All cave systems inhabited by *G. palleucus* within the Central Basin are developed between 180-215 m within the Ordovician Ridley Limestone and are contained within the Central Basin aquifer system (Brahana and Bradley 1986a). Although the Chattanooga Shale represents an effective barrier of vertical dispersal between the Eastern Highland Rim and Central Basin aquifer systems, this layer has been breached along the escarpment of the Eastern Highland Rim and may permit subterranean dispersal between the two aquifers; however, genetic work is required to determine if Central Basin populations are continuous with or isolated from those in the Eastern Highland Rim and western escarpment of the Cumberland Plateau.

Gyrinophilus gulolineatus is known from nine localities (Brandon 1965; Simmons 1975; Caldwell and Copeland 1992 *op. cit.*; this study), including a record from a roadside ditch in McMinn County (Brandon 1965), within the East Tennessee aquifer system (Brahana et al. 1986) in the Valley and Ridge physiographic province. This province is characterized by elongate ridges and valleys that are oriented northeast to southwest and that formed in response to the intense folding and faulting associated with the formation of the Appalachian Mountains (Miller 1974). Geologic formations within the Valley and Ridge range in age from the Cambrian to Silurian with primary cave development occurring within the Holston Formation, Knox Group, and the Maryville Limestone (Moore 1973). Most cave systems inhabited by *G. gulolineatus* are developed along the slopes of ridges underlain by carbonate rock at 210–260 m. Because of the folding and faulting, lateral flow in the permeable formations generally does not occur (Brahana et al. 1986), restricting subterranean dispersal and gene flow (Barr and Holsinger 1985). Likewise, the East Tennessee aquifer system is isolated from the stratigraphic aquifer systems to the west by a zone of faulting that probably acts as a significant barrier for subterranean dispersal between *G. palleucus* and *G. gulolineatus*.

The discovery of populations of *G. palleucus* in 16 caves and *G. gulolineatus* in two caves from which they were previously unknown substantiates the hypotheses of past workers that the then current ranges of these taxa were an artifact of collection, rather than a depiction of the true range of the complex (Brandon 1967a; Cooper and Cooper 1968; Simmons 1975). Range maps often portray the distributions as a series of disjunct populations as the entrances to supporting caves are plotted individually. This mapping technique disguises the interconnectedness of the subterranean aquatic environment, particularly in stratigraphic carbonates west of the Valley and Ridge. Furthermore, Curl (1966) indicates that as few as 5% of limestone caves in the

temperate regions have openings large enough for humans to enter. Because neither *G. palleucus* nor *G. gulolineatus* are restricted to subterranean water accessible to humans, we suggest that their populations are distributed throughout the subterranean waters of the drainage systems they inhabit. Therefore, populations of *G. gulolineatus* and *G. palleucus* extend more-or-less continuously within subterranean waters associated with the Tennessee River watershed as the river flows through Walden Ridge in Hamilton Co., Tennessee, into and through north Alabama and northward into Tennessee. Although *G. palleucus* has been observed in caves along the Tennessee River in extreme northwest Alabama (e.g., McKinney Pit Cave in Colbert Co.), records are lacking from caves within the Cumberland Plateau proper and Western Highland Rim, indicating that additional survey work is required to ascertain the distribution of *Gyrinophilus* species within each of these latter provinces. Furthermore, genetic analyses requiring thorough sampling of existing localities throughout the range of the *G. palleucus* complex are required in order to discern the extent of connectivity among populations.

Determining the distribution of each member of the complex proved more difficult, largely because the systematics and taxonomy of the complex have not been analyzed or revised substantially since the monographic work of Brandon (1966) who used morphological traits (coloration and number of trunk vertebrae) to distinguish the three described taxa. As originally described, each recognized taxon has a small, allopatric distribution (McCrary 1954; Lazell and Brandon 1962; Brandon 1967a), with *G. p. palleucus* limited to caves in the Crow Creek drainage system in Franklin Co., Tennessee, *G. p. necturoides* restricted to the Big Mouth-Big Room Cave system in the Elk River drainage system in Grundy Co., Tennessee, and *G. gulolineatus* associated with caves in the Valley and Ridge physiographic province of east Tennessee. The ranges of these taxa were determined when very few populations were known and ascertaining the relationship of newly discovered populations to the established taxa is often difficult; consequently, populations found outside the originally described ranges rarely are assigned to any of the three recognized taxa. For example, Tom C. Barr found *G. palleucus* inhabiting caves in the Stones River watershed of Rutherford Co., thereby extending the distribution of the complex into the Central Basin of Tennessee (Brandon 1966, 1967a). Decades later, Miller and Walther (1994) extended the Stones River watershed/Central Basin distribution northeastward into Wilson Co., Tennessee. Samoray and Garland (2002) also found a new population to the south in Bedford Co., but the population they reported was associated with the Duck River watershed. The Duck River flows westward from the Central Basin into the Western Highland Rim before entering into the Tennessee River; whereas, the Stones

River flows northward, remaining entirely within the Central Basin, into the Cumberland River. Although known for decades, the Central Basin populations never have been associated with any of the described taxa, and some authorities suggest that these populations could represent an undescribed taxon (Brandon 1966; Redmond and Scott 1996). Similarly, Cooper (1968) and Miller (1995) greatly increased the known distribution of the *G. palleucus* complex when they reported populations in northwest Georgia, north Alabama, and south-central Tennessee (e.g., Nickajack Cave in Marion Co), and in the Collins River watershed in the eastern Highland Rim of Warren Co., Tennessee, respectively. Generally, neither the northwest Georgia nor Collins River populations are assigned to a subspecies (Cooper 1968; Buhlmann and Wynn 1996; Buhlmann 2001; but see Petranka 1998). Several populations in northeastern Alabama reportedly are intergrades between *G. p. palleucus* and *G. p. necturoides* because they possess morphological features intermediate between these two subspecies (Lazell and Brandon 1962; Brandon 1966; 1967a; Cooper and Cooper 1968; Mount 1975; Godwin 2000 *op. cit.*). Regardless of past confusion, the discovery of populations outside known ranges raises doubts as to the purported allopatric distributions of the three taxa and clearly shows the need for a detailed systematic analysis of the complex. Consequently, until genetic analyses are complete, we are hesitant to assign most newly discovered populations to any of the recognized taxa. This essentially is the same stance taken by past workers.

Inferring Population Size.—Based on the number of individuals found during surveys, most populations of Tennessee Cave Salamanders are reportedly small (Simmons 1975; Petranka 1998; Beachy 2005a,b). This assumption is reinforced by the observation of Simmons (1975) and often restated by others that *G. palleucus* and *G. gulolineatus* have low vagility and are found often in the exact location on subsequent searches months later. Time constraints prevented us from performing mark-recapture studies at each cave; consequently, we infer relative population size based on the number of salamanders found during each survey. We acknowledge inherent flaws in such an inference; perhaps the most significant is the assumption that populations are restricted to cave streams. Nonetheless, we used the same techniques to search each cave and, therefore, assume our success corresponds to the relative abundance of salamanders inhabiting them. Our relatively consistent success in caves searched multiple times supports this assumption, at least when making broad generalities. For example, we routinely found more than 20 salamanders during favorable collecting conditions in Big Mouth, Sinking Cove, Cave Cove, and

Custard Hollow caves; whereas, we consistently found six or fewer salamanders in Herring, Pompie, Gallagher, and Mudflats caves. Thus, some caves either support larger populations than others, or perhaps equally likely, individuals in some populations enter into the cave streams accessible to humans more frequently than individuals inhabiting other subterranean systems. The differences in relative abundance among caves warrant further discussion because of the bearing on conserving populations.

Relatively Large Populations (High-density Caves).—Caves associated with the Crow Creek drainage system in southern Franklin Co. (Cave Cove Cave, Sinking Cove Cave, and Custard Hollow Cave) support relatively high-density populations of Tennessee Cave Salamanders. Several investigators have reported finding many individuals (>20) during single day searches in these caves (Brandon 1966; Simmons 1975; Caldwell and Copeland 1992) and the populations contained therein appear to be stable, showing no obvious declines during the last 40 years (Brandon 1966; Caldwell and Copeland 1992; this study). Caldwell and Copeland (1992) suggest a correlation between the occurrence of Tennessee Cave Salamanders and inflow (sinkhole) cave systems. The inflow systems presumably provide a relatively constant nutrient source and thereby provide a food base for salamanders. While measuring SVL and TL, we often noted isopods in the stomach of the salamanders and an occasional salamander regurgitated epigeal invertebrates, such as earthworms and coleopteran larvae. Although larger prey items, including conspecifics, have been reported (Brandon 1967b; Simmons 1975), relatively small prey, such as earthworms, isopods and amphipods, are frequently consumed by *G. palleucus* (Brandon 1967b). The streambed of many of the inflow caves we searched (e.g., Big Mouth Cave and Cave Cove Cave) was littered with organic matter washed in from the epigeal environment, including decomposing leaves and twigs. During our surveys of these caves, we noted that isopods were abundant within the organic matter and on the undersurface of rocks; conversely, we noted relatively few isopods in those systems with little organic matter. Possibly, the relative abundance of Tennessee Cave Salamanders is associated with relative abundance of organic matter. However, we found relatively few salamanders in some nutrient rich caves, including Crystal Cave and Herring Cave. Although bats were found in nearly all caves searched, a few caves supported Gray Bat (*Myotis grisescens*) maternity or bachelor colonies (e.g., Herring, Lusk, Trussell, and Jaco Spring caves). The large numbers of bats in these colonies deposit a significant amount of organic matter in the caves. Although Tennessee Cave Salamanders inhabit each of these caves, none appear to support large

populations, at least in comparison to the high-density caves mentioned above. More work is required to determine why some nutrient rich caves support relatively larger populations than other nutrient rich caves.

Relatively Small Populations (Low-density Caves).—Relatively low abundance of Tennessee Cave Salamanders was characteristic of all Central Basin, Warren Co., Marion Co., northwest Georgia, several Grundy Co., and nearly all Valley and Ridge caves. Indeed, the numbers of salamanders found in these caves are too low to sustain breeding populations, indicating that the populations extend beyond human-accessible cave stream channels. For example, we found two or fewer individuals in eleven of the 30 supporting caves, and five or fewer individuals during any search in five additional supporting caves. These low numbers suggest that the salamanders are not permanent residents of the cave stream; rather, they inhabit subterranean water not readily accessible to humans and, perhaps, only rarely enter into the cave stream. Consequently, these populations are discovered when salamanders venture or are washed into a stream channel from their more inaccessible haunts. Movement into cave streams from more inaccessible subterranean waters has been suggested for the Southern Cavefish, *Typhlichthys subterraneus*, in the Ozarks of Missouri (Noltie and Wicks 2001). Such habitat use can, in part, explain the rare sighting in a cave visited often, and our varied success in finding salamanders in several caves that we surveyed multiple times (e.g., Lusk, Gourneck, Trussell, Gallagher, and Garner Spring caves). In addition to strengthening our argument that the salamanders are not necessarily regular inhabitants of cave streams accessible to humans, our varied success in finding salamanders in caves searched on multiple occasions indicates that a single survey of a cave, even when thorough and conducted by the same individuals, is not necessarily sufficient for verifying the existence of populations in that cave system. For example, we found two *G. palleucus* during our second survey of Garner Spring Cave, but none during our other surveys. Also, we found salamanders during our first and second search of both Lusk and Gallagher caves, but none during our third searches. Moreover, we were unsuccessful in locating *G. palleucus* in both Gourneck and Trussell caves during our first two surveys, but found one individual during our third survey of each cave.

Because of our inability to find salamanders in caves known to support populations, we suspect that Tennessee Cave Salamanders inhabit many caves that we surveyed unsuccessfully. For example, we were unsuccessful in documenting extant populations in several historic sites, including Jackson, Buggytop, McFarland, McKinney Pit, Pattons, Ranie Willis, Shelta,

and Yell caves; however, we are reticent to declare these populations extirpated, as few salamanders have been reported from these caves. Rather, we suggest the occasional or rare sighting of salamanders in these caves strengthens our hypothesis that salamanders inhabit subterranean waters other than those streams accessible to humans.

Range-wide Population Declines.—Although census data are used to monitor some vertebrate populations (e.g., breeding bird surveys), including salamanders (Highton 2005), the suitability of this technique has received criticism (Schmidt et al. 2002; Schmidt 2003, 2004; Bailey et al. 2004). Regardless of the statistical suitability, census data have been used to determine relative abundance and possible population fluctuations of the Tennessee Cave Salamander complex (Caldwell and Copeland 1992). Also, estimates of population size based on mark-recapture studies rarely have been conducted on any member of the complex (but see Simmons 1975; Petranka 1998). Because of the difficulty in capturing enough salamanders to conduct mark-recapture studies at most localities, census data is the only measure available to estimate fluctuations in population size through time. The reported decline in all populations of members of the Tennessee Cave Salamander complex (Beachy 2005a,b) stems from comparing counts from earlier and more recent surveys. Because relatively few individuals have been found in more recent surveys compared to those conducted decades ago, the populations are reported to be in decline (Caldwell and Copeland 1992; Petranka 1998; Beachy 2005a,b). However, we found more salamanders than previous workers at several historic sites. We do not know if our relatively more successful searches are associated with improved search techniques, differences in seasonality of searches, or truly reflective of changes in population size. Nonetheless, if we use census data to estimate trends in population size, we come to very different conclusions than previous authors. Although we recognize the threats posed to the presumed fragile ecosystems of subterranean streams, rather than decreasing range wide, populations of Tennessee Cave Salamanders are either relatively stable (Franklin Co. caves and Mudflats Cave) or increasing (Big Mouth Cave).

Conservation Implications.—The worldwide decline in amphibian populations has received considerable attention during the past two decades. Several factors have been associated with the declines, including ultraviolet radiation, habitat destruction, pollution, disease, and over-collection (Blaustein et al. 1997; Alford and Richards 1999; Semlitsch 2003). Many species of obligate cave-dwelling salamanders are characterized by small distributions (often restricted to a

single cave system) and low-density populations (Chippindale 2000; Chippindale et al. 2000; Beachy 2005a,b) and, therefore, are particularly susceptible to decline. Elliott (2000) provides a summary of threats to caves and karst communities, many of which apply to caves harboring populations of Tennessee Cave Salamanders. Chippindale and Price (2005) summarize the threats to cave-dwelling salamanders of the Edwards Plateau region of Texas, but specific threats to species in other regions have received comparatively little attention. However, habitat degradation likely poses the greatest and most immediate threat to Tennessee Cave Salamander populations. In particular, agricultural and silvicultural practices, and urbanization adversely affect water quality by increasing herbicide and pesticide load, silt load, and exhaust runoff from roads. Unfortunately, limited water quality data exist for most subterranean waters in Tennessee in general, and for caves inhabited by *G. palleucus* and *G. gulolineatus* specifically. In many instances, the source of the water supplying the underground streams is poorly understood. However, because of their proximity to downtown Knoxville (e.g., Meade Quarry and Mudflats caves are located within residential housing developments, and construction of roads and residential housing developments are occurring on the land surrounding Christian and Aycock Spring caves), the Knox Co. populations of *G. gulolineatus* in particular are in jeopardy. Similarly, the Rutherford and Wilson Co. populations of *G. palleucus* are in expanding urban areas and are likely to be negatively impacted by urban development.

Based on the number of individuals reported in past studies (Brandon 1966; Caldwell and Copeland 1992; Petranka 1998), several caves in the Crow Creek drainage of Franklin Co., Tennessee, support relatively large populations. For example, Brandon found approximately 60 *G. p. palleucus* during a two-day search of Custard Hollow Cave in November 1961. However, Caldwell and Copeland (1992) were unable to locate any salamanders during their August 1990 search of the cave and expressed concern about the possible decline of the population. Their concern is cited as a reason for conservation listing of the species (IUCN 2004, op cit.; Beachy 2005b). However, we searched the cave twice and found 25 *G. palleucus* during the first survey and 41 during the second survey. Although fewer than reported by Brandon (op. cit.) we found a diversity of size classes, indicating reproduction and recruitment are successfully occurring at Custard Hollow Cave.

Particular concern has been expressed also for the fate of *G. p. necturoides*, which is listed as "Critically Imperiled" (G2G3T1) by NatureServe (NatureServe. 2006, op. cit.) and "Vulnerable" by the IUCN (IUCN 2004, op. cit.). Lazell and Brandon (1962) stated that *G. p. necturoides* was abundant in Big Mouth Cave, but

Simmons (1975) found very few salamanders during the early 1970s and suggested that the population was declining and could be extirpated within 25 years. A few individuals were found during the 1980s and early 1990s (Caldwell and Copeland 1992), but the population was reportedly small. We found substantially more salamanders than previous investigators and our data indicate that the population has rebounded from the low numbers reported during the past 30 years. Although we did not find eggs, we found small larvae, and a variety of larger size classes. Rather than declining, or even remaining stable at a small population size, we suggest that the population is relatively large and, based on census data, has increased tremendously since the 1970s. Also, the discovery of additional populations within the Elk River watershed suggests that *G. p. necturoides* may be more widespread than previously thought.

Metamorphosed Tennessee Cave Salamanders.—Although Tennessee Cave Salamanders are paedomorphic, a few metamorphosed individuals have been reported, including a *G. gulolineatus* from Mudflats Cave (Simmons 1976), and *G. p. palleucus* from Sinking Cove Cave (Yeatman and Miller 1985) and Custard Hollow Cave (Brandon et al. 1986). Miller (1995) collected a metamorphosed *G. palleucus* from a spring along the Collins River south of McMinnville, Tennessee. This individual was collected following heavy rains that presumably washed the salamander out of the subterranean stream. Additionally, one of the two individuals collected from a spring at Stone Cave and identified as *G. palleucus* by Hollingsworth et al. (1997) transformed shortly after capture. However, the eyes are relatively large and the irises clearly visible in the larvae at Stone Cave, prompting us to identify these salamanders as *G. porphyriticus*.

During this study, we found metamorphosed *Gyrinophilus* at three caves: Cruze Cave, Meade Quarry Cave, and Jess Elliot Cave. The population inhabiting Cruze Cave was identified historically as *G. gulolineatus* (Caldwell and Copeland 1992). However, we observed a large proportion of metamorphosed individuals (23%). Furthermore, the larvae from this population exhibit varying degrees of throat pigmentation, head shape, eye size, and iris distinction. The propensity to metamorphose, relatively large eye size and iris presence in the salamanders at Cruze Cave lead us to identify these salamanders as *G. porphyriticus*, rather than as *G. gulolineatus*. Three metamorphosed salamanders were observed at Meade Quarry Cave, but did not resemble the metamorphosed individuals from nearby Cruze Cave. Likewise, two metamorphosed salamanders were observed from Jess Elliot Cave in Jackson Co., Alabama. These latter five individuals differed from metamorphosed *G. porphyriticus* in aspects of cranial morphology and extent of eye development.

Morphological and genetic comparisons of transformed and larviform individuals are ongoing.

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APPENDIX. Caves searched for *Gyrinophilus* from April 2004 – June 2007. Caves are arranged by watershed and physiographic province. Caves that are historic localities for *G. palleucus* or *G. gulolineatus* are indicated in bold.

Date	Cave Name	Cave No.	County	State	Ggul	Gpal	Gpor
Buffalo River: Western Highland Rim							
07/22/06	Cave Branch Cave	THI3	Hickman	TN	0	0	0
07/22/06	Allens Creek Cave	TLS3	Lewis	TN	0	0	0
07/22/06	Greer Hollow Cave	TPR50	Perry	TN	0	0	0
Caney Fork River: Cumberland Plateau							
10/02/05	Camps Gulf Cave No. 2	TVB197	Van Buren	TN	0	0	0
01/09/06	Upper Sheep Cave	TWH42	White	TN	0	0	0
01/09/06	Virgin Falls Cave	TWH43	White	TN	0	0	0
07/09/06	Wes Allen Cave	TWH500	White	TN	0	0	0
01/09/06	Big Laurel Creek Cave	TWH51	White	TN	0	0	0
Caney Fork River: Eastern Highland Rim							
04/27/05	Gar Island Cave	TDK90	DeKalb	TN	0	0	6
09/19/04	Martha Wright Cave	TDK92	DeKalb	TN	0	0	0
09/19/04	Pauley Cave	TDK95	DeKalb	TN	0	0	2
10/24/04	West Cemetery Cave	TPU418	Putnam	TN	0	0	7
05/28/06	Sebowisha Cave	TSM68	Smith	TN	0	0	0
12/28/04	Indian Cave	TWH17	White	TN	0	0	0
12/28/04	Witt Cave	TWH844	White	TN	0	0	0
Clinch River: Valley and Ridge							
09/17/05	Aycock Spring Cave	TKN172	Knox	TN	1	0	0
09/17/05	Christian Cave	TKN49	Knox	TN	1	0	0
12/30/05	Eblen Cave	TRN6	Roane	TN	0	0	0
Collins River: Cumberland Plateau							
03/06/05	Blowing Cave	TWR4	Warren	TN	0	0	0
06/16/07	Blowing Cave	TWR4	Warren	TN	0	0	0
Collins River: Eastern Highland Rim							
02/09/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
02/26/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
09/15/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
10/15/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
10/29/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
12/02/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
12/20/05	Gunters Cave	TCN35	Cannon	TN	0	0	0
01/28/06	Gunters Cave	TCN35	Cannon	TN	0	0	0
09/30/06	Gunters Cave	TCN35	Cannon	TN	0	0	0
01/26/05	Gunters Cave	TCN35	Cannon	TN	0	0	1
12/20/05	Pond Cave	TCN63	Cannon	TN	0	0	0
12/16/04	Cow Cave	TWR286	Warren	TN	0	0	0
09/04/04	King Cave	TWR295	Warren	TN	0	3	0
06/22/05	King Cave	TWR295	Warren	TN	0	3	0
09/04/04	Old Folks Cave	TWR299	Warren	TN	0	0	0
06/22/05	Old Folks Cave	TWR299	Warren	TN	0	0	0
12/16/04	Sugarcookie Cave	TWR301	Warren	TN	0	1	0
08/05/04	Cable Cave	TWR310	Warren	TN	0	0	0
08/05/04	Jaco Spring Cave	TWR317	Warren	TN	0	1	0
08/05/04	York Cave	TWR332	Warren	TN	0	0	0
Cumberland River: Central Basin							
05/28/06	Flat Rock Cave	TSM66	Smith	TN	0	0	0
Cumberland River: Cumberland Plateau							
05/12/07	Neely Creek Cave		Pulaski	KY	0	0	0
05/12/07	Sloans Valley Cave		Pulaski	KY	0	0	0
Cumberland River: Eastern Highland Rim							
05/28/06	Barlett Cave	TPU2	Putnam	TN	0	0	0
03/08/07	Hidden Cave	TJK58	Jackson	TN	0	0	0
03/08/07	Pilot Knob Cave	TJK32	Jackson	TN	0	0	0
Duck River: Central Basin							
06/18/05	Berlin Spring Cave	TMS10	Marshall	TN	0	0	0
01/02/06	Gallagher Cave	TMS23	Marshall	TN	0	0	0
06/18/05	Gallagher Cave	TMS23	Marshall	TN	0	1	0
08/09/05	Gallagher Cave	TMS23	Marshall	TN	0	3	0

Miller and Niemiller.—Tennessee Cave Salamanders in Tennessee

06/18/05 Gallagher Cave South TMS24 Marshall TN 0 0 0
APPENDIX. Continued.

Date	Cave Name	Cave No.	County	State	Ggul	Gpal	Gpor
06/18/05	Pompie Cave	TMU19	Maury	TN	0	1	0
01/02/06	Pompie Cave	TMU19	Maury	TN	0	1	0
06/16/06	Pompie Cave	TMU19	Maury	TN	0	5	0
08/09/05	Pompie Cave	TMU19	Maury	TN	0	6	0
Duck River: Eastern Highland Rim							
04/06/04	Yell Cave	TBE16	Bedford	TN	0	0	0
08/18/04	Harrison Springs Cave	TBE23	Bedford	TN	0	0	0
04/20/06	Warren Springs Cave	TBE40	Bedford	TN	0	0	0
Elk River: Cumberland Plateau							
10/02/04	Blowing Springs Cave	TCF18	Coffee	TN	0	19	0
08/25/04	Welch Cave	TCF60	Coffee	TN	0	0	0
03/11/05	Lusk Cave	TCF8	Coffee	TN	0	0	0
08/25/04	Lusk Cave	TCF8	Coffee	TN	0	3	0
08/26/05	Lusk Cave	TCF8	Coffee	TN	0	3	0
10/18/04	Lusk Cave	TCF8	Coffee	TN	0	11	0
05/10/05	Walker Spring Cave	TFR28	Franklin	TN	0	0	0
05/12/05	Crystal Cave	TGD10	Grundy	TN	0	1	0
11/21/06	Crystal Cave	TGD10	Grundy	TN	0	1	0
08/28/04	Trussell Downstream Cave	TGD132	Grundy	TN	0	0	0
09/28/04	Trussell Downstream Cave	TGD132	Grundy	TN	0	0	0
11/14/06	Trussell Downstream Cave	TGD132	Grundy	TN	0	0	0
11/21/06	Trussell Downstream Cave	TGD132	Grundy	TN	0	0	0
05/25/05	Elkhead Shelter Cave	TGD165	Grundy	TN	0	0	0
06/29/04	Big Mouth Cave	TGD2	Grundy	TN	0	12	0
03/10/07	Big Mouth Cave	TGD2	Grundy	TN	0	19	0
04/16/06	Big Mouth Cave	TGD2	Grundy	TN	0	23	0
08/25/05	Big Mouth Cave	TGD2	Grundy	TN	0	24	0
11/10/05	Big Mouth Cave	TGD2	Grundy	TN	0	26	0
04/17/05	Big Mouth Cave	TGD2	Grundy	TN	0	27	0
01/26/05	Big Mouth Cave	TGD2	Grundy	TN	0	28	0
06/16/05	Big Mouth Cave	TGD2	Grundy	TN	0	30	0
07/21/04	Big Mouth Cave	TGD2	Grundy	TN	0	31	0
07/15/06	Big Mouth Cave	TGD2	Grundy	TN	0	32	0
02/06/05	Big Mouth Cave	TGD2	Grundy	TN	0	34	0
03/10/05	Big Mouth Cave	TGD2	Grundy	TN	0	34	0
11/21/06	Trussell Cave	TGD26	Grundy	TN	0	0	0
12/17/06	Trussell Cave	TGD26	Grundy	TN	0	0	0
08/28/04	Trussell Cave	TGD26	Grundy	TN	0	0	0
09/28/04	Trussell Cave	TGD26	Grundy	TN	0	0	0
11/14/06	Trussell Cave	TGD26	Grundy	TN	0	1	0
05/25/05	Red Trillium Cave	TGD292	Grundy	TN	0	0	0
07/07/04	Big Room Cave	TGD3	Grundy	TN	0	0	0
05/25/05	Mulepen Spring Cave	TGD60	Grundy	TN	0	0	0
12/22/04	Smith Hollow Cave	TGD64	Grundy	TN	0	2	0
08/19/04	Smith Hollow Cave	TGD64	Grundy	TN	0	3	0
Elk River: Eastern Highland Rim							
05/20/07	Powers Cave	TFR292	Franklin	TN	0	0	0
04/20/06	Billy Stone Cave	TMR1	Moore	TN	0	0	0
Lower Tennessee River: Cumberland Plateau							
01/13/07	Talley Ditch Cave	AJK248	Jackson	AL	0	0	0
01/13/07	Bluff River Cave	AJK2800	Jackson	AL	0	11	0
12/18/06	Jess Elliot Cave	AJK323	Jackson	AL	0	21	0
01/28/07	Guess Creek Cave	AJK593	Jackson	AL	0	0	0
01/27/07	McFarland Cave	AJK65	Jackson	AL	0	0	0
01/27/07	Tony Sinks Cave	AJK78	Jackson	AL	0	24	0
05/07/07	Lacon Exit Cave	AMG3342	Morgan	AL	0	0	1
05/09/07	Beech Spring Cave	AMS347	Marshall	AL	0	0	0
09/07/06	Long's Rock Wall Cave	GDD101	Dade	GA	0	0	0
04/13/06	Hurricane Cave	GDD62	Dade	GA	0	0	2
10/20/05	Fricks Cave	GWK14	Walker	GA	0	1	0
09/07/06	Roger Branch Cave	GWK204	Walker	GA	0	0	0
10/20/05	Pettyjohns Cave	GWK29	Walker	GA	0	0	0
10/20/05	Anderson Spring Cave	GWK46	Walker	GA	0	0	10
04/13/06	Pigeon Cave	GWK57	Walker	GA	0	0	4

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06/09/04 **Buggytop Cave** TFR16 Franklin TN 0 0 0
 APPENDIX. *Continued.*

Date	Cave Name	Cave No.	County	State	Ggul	Gpal	Gpor
10/18/04	Buggytop Cave	TFR16	Franklin	TN	0	0	0
08/28/04	Garner Spring Cave	TFR199	Franklin	TN	0	0	0
08/06/06	Garner Spring Cave	TFR199	Franklin	TN	0	0	0
08/13/06	Garner Spring Cave	TFR199	Franklin	TN	0	0	0
08/02/06	Garner Spring Cave	TFR199	Franklin	TN	0	2	0
08/03/05	Ranie Willis Cave	TFR20	Franklin	TN	0	0	0
08/02/06	Ranie Willis Cave	TFR20	Franklin	TN	0	0	0
08/06/06	Salt River Cave	TFR23	Franklin	TN	0	1	0
05/20/07	Salt River Cave	TFR23	Franklin	TN	0	1	0
08/10/04	Sinking Cove Cave	TFR25	Franklin	TN	0	24	0
06/09/05	Sinking Cove Cave	TFR25	Franklin	TN	0	24	0
08/16/04	Sinking Cove Cave	TFR25	Franklin	TN	0	25	0
08/16/04	Waterfall Cave	TFR29	Franklin	TN	0	0	0
09/06/05	Mill Creek Cave	TFR313	Franklin	TN	0	0	0
02/20/05	Cave Cove Cave	TFR33	Franklin	TN	0	30	0
07/21/05	Cave Cove Cave	TFR33	Franklin	TN	0	41	0
08/11/04	Custard Hollow Cave	TFR7	Franklin	TN	0	25	0
06/08/05	Custard Hollow Cave	TFR7	Franklin	TN	0	41	0
06/09/04	Tom Pack Cave	TFR87	Franklin	TN	0	0	0
12/23/06	Raccoon Mountain Cave	THM4	Hamilton	TN	0	0	7
12/22/05	Gourdneck Cave	TMN14	Marion	TN	0	0	0
06/08/06	Gourdneck Cave	TMN14	Marion	TN	0	0	0
08/13/06	Gourdneck Cave	TMN14	Marion	TN	0	1	0
12/17/06	Honeycutt Cave	TMN16	Marion	TN	0	0	0
04/21/07	Lost Pig Cave	TMN20	Marion	TN	0	4	0
05/04/05	Shakerag Cave	TMN371	Marion	TN	0	1	0
12/17/06	Bible Springs Cave	TMN91	Marion	TN	0	0	0
Lower Tennessee River: Highland Rim							
05/08/07	Elbow Cave	ACE1054	Colbert	AL	0	0	0
05/08/07	Bell Cave	ACE1055	Colbert	AL	0	0	0
05/08/07	McKinney Pit Cave	ACE629	Colbert	AL	0	0	0
05/08/07	White Spring Cave	ALM242	Limestone	AL	0	0	0
05/09/07	Shelta Cave	AMD4	Madison	AL	0	0	0
Lower Tennessee River: Western Highland Rim							
07/17/05	Baugus Cave	TDC1	Decatur	TN	0	0	0
07/17/05	Cody Cave	TDC17	Decatur	TN	0	0	0
07/17/05	Hornet Cave	TDC19	Decatur	TN	0	0	0
07/17/05	Baby Cave	TDC7	Decatur	TN	0	0	0
07/02/06	Jerrolds Cave	THR15	Hardin	TN	0	0	0
07/02/06	Pickwick Pot	THR4	Hardin	TN	0	0	0
Obed River: Cumberland Plateau							
03/05/06	Baker Cave	TCD1	Cumberland	TN	0	0	0
03/05/06	Spencer Rock Cave	TCD11	Cumberland	TN	0	0	3
Obey River: Eastern Highland Rim							
07/30/05	Marcus Minimus Cave	TPI153	Pickett	TN	0	0	0
07/30/05	Marcus Cave	TPI76	Pickett	TN	0	0	14
07/30/05	Mark Us Cave	TPI77	Pickett	TN	0	0	6
07/30/05	Ringing Rock River Cave	TPI84	Pickett	TN	0	0	1
Sequatchie River: Cumberland Plateau							
12/22/05	Wine Cave	TMN141	Marion	TN	0	0	0
08/13/06	Sequatchie Cave	TMN179	Marion	TN	0	0	0
06/08/06	Ship Cave	TMN39	Marion	TN	0	0	0
06/19/05	Keyhole Cave	TSQ15	Sequatchie	TN	0	0	0
06/19/05	Wilmoth Cave	TSQ5	Sequatchie	TN	0	0	0
Sequatchie River: Sequatchie Valley							
08/13/06	Stone Cave	TSQ7	Sequatchie	TN	0	0	0
12/23/06	Stone Cave	TSQ7	Sequatchie	TN	0	0	0
06/19/05	Stone Cave	TSQ7	Sequatchie	TN	0	0	1
12/17/06	Stone Cave	TSQ7	Sequatchie	TN	0	0	4
Stones River: Central Basin							
11/11/04	Swirl Canyon Cave	TDA46	Davidson	TN	0	0	0
08/04/04	Patterson Cave	TRU11	Rutherford	TN	0	0	0

Miller and Niemiller.—Tennessee Cave Salamanders in Tennessee

12/10/05 Patterson Cave TRU11 Rutherford TN 0 0 0
 APPENDIX. *Continued.*

Date	Cave Name	Cave No.	County	State	Ggul	Gpal	Gpor
07/28/04	Pattons Cave	TRU12	Rutherford	TN	0	0	0
07/29/04	Pattons Cave	TRU12	Rutherford	TN	0	0	0
05/03/05	Pattons Cave	TRU12	Rutherford	TN	0	0	0
12/10/05	Pattons Cave	TRU12	Rutherford	TN	0	0	0
03/06/06	Pattons Cave	TRU12	Rutherford	TN	0	0	0
08/07/06	Pattons Cave	TRU12	Rutherford	TN	0	0	0
03/11/07	Pattons Cave	TRU12	Rutherford	TN	0	0	0
08/04/04	Snail Shell Cave	TRU16	Rutherford	TN	0	1	0
07/18/04	Snail Shell Cave	TRU16	Rutherford	TN	0	2	0
07/08/06	Big Oak Chasm	TRU28	Rutherford	TN	0	0	0
08/27/04	Herring Cave	TRU8	Rutherford	TN	0	1	0
06/25/05	Herring Cave	TRU8	Rutherford	TN	0	3	0
07/29/04	Herring Cave	TRU8	Rutherford	TN	0	4	0
07/20/06	Herring Cave	TRU8	Rutherford	TN	0	4	0
06/08/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/10/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/12/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/14/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/16/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/17/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/22/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
11/11/04	Jackson Cave	TWL20	Wilson	TN	0	0	0
05/03/05	Jackson Cave	TWL20	Wilson	TN	0	0	0
05/23/05	Jackson Cave	TWL20	Wilson	TN	0	0	0
06/29/05	Jackson Cave	TWL20	Wilson	TN	0	0	0
09/08/05	Jackson Cave	TWL20	Wilson	TN	0	0	0
07/08/06	Jackson Cave	TWL20	Wilson	TN	0	0	0
05/23/05	Burnt House Cave	TWL35	Wilson	TN	0	0	0
12/18/05	Hurricane Junction Cave	TWL73	Wilson	TN	0	0	0
05/26/05	Cedar Forest Cave	TWL9	Wilson	TN	0	0	0
Stones River: Eastern Highland Rim							
09/21/04	Espey Cave	TCN10	Cannon	TN	0	0	0
05/11/05	Espey Cave	TCN10	Cannon	TN	0	0	0
09/15/05	Henpeck Mill Cave	TCN12	Cannon	TN	0	0	0
08/06/06	Henpeck Mill Cave	TCN12	Cannon	TN	0	0	0
10/16/04	Haws Spring Cave	TCN81	Cannon	TN	0	0	0
05/18/05	Burk Cave	TRU26	Rutherford	TN	0	0	0
Upper Tennessee River: Valley and Ridge							
11/20/04	Ebenezer Rising Cave	TKN150	Knox	TN	0	0	0
10/23/04	Meades River Cave	TKN151	Knox	TN	0	0	0
04/22/07	Meades River Cave	TKN151	Knox	TN	0	0	1
10/23/04	Fifth Entrance Cave	TKN167	Knox	TN	0	0	0
10/31/04	Cruze Cave	TKN24	Knox	TN	0	0	32
01/06/05	Cruze Cave	TKN24	Knox	TN	0	0	36
03/06/05	Cruze Cave	TKN24	Knox	TN	0	0	42
11/19/06	Cruze Cave	TKN24	Knox	TN	0	0	47
09/10/06	Cruze Cave	TKN24	Knox	TN	0	0	60
12/31/05	Cruze Cave	TKN24	Knox	TN	0	0	67
07/18/06	Cruze Cave	TKN24	Knox	TN	0	0	84
10/23/04	Meade Quarry Cave	TKN28	Knox	TN	11	0	0
11/04/06	Meade Quarry Cave	TKN28	Knox	TN	11	0	0
04/22/07	Meade Quarry Cave	TKN28	Knox	TN	14	0	0
11/20/04	Mudflats Cave	TKN9	Knox	TN	5	0	0
01/06/05	Mudflats Cave	TKN9	Knox	TN	3	0	0
12/30/05	Mudflats Cave	TKN9	Knox	TN	5	0	0
11/12/06	Mudflats Cave	TKN9	Knox	TN	2	0	0
06/07/07	Mudflats Cave	TKN9	Knox	TN	5	0	0
03/05/05	Big Cave	TRN13	Roane	TN	0	0	0
03/05/05	Chimney Cave	TRN14	Roane	TN	0	0	0
12/17/04	Berry Cave	TRN3	Roane	TN	1	0	0
03/05/05	Berry Cave	TRN3	Roane	TN	4	0	0
06/07/07	Cave Creek Cave	TRN5	Roane	TN	0	0	1
04/05/07	Steamboat Crawl	TKN173	Knox	TN	0	0	0