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Salamanders of the Mio-Pliocene Gray Fossil Site, Washington County, Tennessee.

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Salamanders of the Mio-Pliocene Gray Fossil Site, Washington County, Tennessee

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Master of Science in Biological Sciences

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by

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May 2009

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ABSTRACT

Salamanders of the Mio-Pliocene Gray Fossil Site, Washington County, Tennessee

by

Grant Stanley Boardman

Screening efforts at the Gray Fossil Site, Washington County, Tennessee, have yielded a unique and diverse salamander fauna for the southern Appalachian Mio-Pliocene; including at least five taxa from three modern families (Ambystomatidae, Plethodontidae, and Salamandridae) supporting the woodland-pond interpretation of the site. All specimens represent the earliest record of their respective families in the Appalachian Mountains; with the *Notophthalmus* sp. vertebrae being the only Mio-Pliocene skeletal fossil known for the family Salamandridae in North America. Three types of plethodontid salamander are present, with one type representing the earliest known desmognathine. The desmognathine fossils lend credence to the 'Appalachian' origin of the clade in the Mio-Pliocene. The GFS salamander fauna is predominated by plethodontids; competition is inferred by the presence of several similarly large-sized taxa and is invoked to explain the presence of neotenic individuals in an otherwise amicable terrestrial environment.

DEDICATION

This thesis is dedicated to my mother, Gail Ann Hill Boardman, who passed away in July 1998 from complications with Multiple Sclerosis.

I also dedicate this thesis to my beautiful wife, Patricia Lee, without her patience, understanding, and enthusiasm I wouldn't have made it this far in one piece; and to Dr. Judith A. Schiebout, my long-time mentor and friend who taught me the ropes of Paleontology and never stopped believing in me.

To the three most important women in my life, this is for you.

ACKNOWLEDGMENTS

Many thanks to the Departments of Biological Sciences and Geosciences at East Tennessee State University for working in conjunction to provide a paleontology program to graduate students. Thanks are also due to the ETSU and General Shale Brick Natural History Museum at the Gray Fossil Site for providing access to the fossil specimens examined and to all the volunteers who worked to find and prepare these specimens. I also thank my advisor and committee chair, Blaine W. Schubert, for allowing me to take on this project and all the guidance he has given me. I am indebted to my other committee members (Steve Wallace, Tom Laughlin, and Jim Mead) for their suggestions and guidance. Thanks to Jim Mead, Wayne Van Devender, Dennis Parmley, and Blaine Schubert for access to modern salamander specimens from their personal collections. I am also indebted to the New Jersey State Museum and Carnegie Museum of Natural History for loan of modern specimens. Thanks to my friends Shawn Haugrud and Brian Compton in the GFS Prep Lab for their witty humor and motivating attitudes. Thanks also to Chris Bell and Jennifer Olori at UT Austin for reprints and helpful comments over the last few years. Thanks to Keila Bredehoeft and Lisa Schaaf, my 'salamander cohorts', for helping to push me along and allowing me to impart what knowledge I have gained regarding salamander osteology.

Financial support was provided by the ETSU Graduate Council Research Grant, Graduate Assistantship in Biological Sciences, and an NSF GK-12 Fellowship (National Science Foundation, Division of Graduate Education GK-12 Program, grant number DGE-074236).

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CHAPTER 1

INTRODUCTION

Salamanders (Order Caudata) are amphibians that have tails (see Figure 1.1), a general characteristic that separates them from the other living amphibian orders: Anura (Frogs and toads), which only have tails in their larval stage, and Gymnophiona (Caecilians), which have highly reduced tails (Duellman and Trueb, 1994). Salamander tails are generally equal in length to the body (except in *Amphiuma* which has an elongate body and short tail), though some have extraordinarily long tails exceeding the length of their bodies (Duellman and Trueb, 1994; Holman, 2006). All salamanders also have four limbs of generally equal size, except the members of the Sirenidae that lack hindlimbs (Duellman and Trueb, 1994). Salamanders, as ectotherms with permeable skin, inhabit regions of high ambient moisture and moderate temperatures to curtail water loss (and assist subcutaneous respiration in lungless taxa like plethodontids) and control body temperature (Duellman and Trueb, 1994). Following Larson et al. (2006), Order Caudata is comprised of 10 living families: Hynobiidae (Asiatic Salamanders), Cryptobranchidae (Hellbenders and Giant Salamanders), Salamandridae (Newts), Plethodontidae (Lungless Salamanders), Rhyacotritonidae (Torrent Salamanders), Amphiumidae (Congo Eels), Ambystomatidae (Mole Salamanders), Proteidae (Mudpuppies, Waterdogs, and Olms), Dicamptodontidae (Pacific Giant Salamanders), and Sirenidae (Sirens) (Duellman and Trueb, 1994). All families, except Hynobiidae, have species that are found in North America (Duellman and Trueb, 1994). Of the modern families found in North America all except Rhyacotritonidae have representatives in the fossil record (Holman, 2006). Two enigmatic salamander families appear in the North American fossil record and are now extinct: the Late Cretaceous to Early Eocene Scapherpetontidae and the Late Cretaceous to Late Miocene Batrachosauroididae

(Holman, 2006).

Fossil sites of Mio-Pliocene age (8 to 4 Ma) in the eastern United States are exceedingly rare outside the state of Florida (see Figure 1.2) and, until recently, were completely absent in the Appalachian Mountains (Wallace and Wang, 2004). Bearing this in mind the discovery of the Gray Fossil Site (GFS), a fossiliferous sinkhole deposit, in the year 2000 was of manifold importance. The Gray Fossil Site not only fills a geographic and temporal gap in the eastern U.S. but also provides the opportunity to study a brief geologic moment in the biological history of the southern Appalachians (Figure 1.3) as the only Mio-Pliocene site in the mountain range. Recovery of microvertebrate remains has for the most part been overlooked in eastern fossil sites. As pointed out by Miller (1992) and Holman (2006), salamander bones are generally small and have low preservation potential (especially in acidic depositional environments), and practically no recovery potential when fossil bearing sediments are not purposefully screened for microvertebrate remains. Even in situations in which screening takes place, salamander bones tend to be overlooked or undersampled when using screen sizes larger than 1/8 inch (Miller, 1992), with these situations completely excluding remains from the smaller salamander taxa.

Five salamander families are recorded in the Mio-Pliocene fossil record in North America: Sirenidae, Plethodontidae, Ambystomatidae, Salamandridae, and the last appearance of the Batrachosauroididae (Holman, 2006). The family Sirenidae is represented by two modern genera, *Siren* and the first fossil appearance of *Pseudobranchus*, both from Florida (Estes, 1981; Holman, 2006). Lungless Plethodontidae are represented by two living genera from California, *Aneides* and *Batrachoseps* (Clark, 1985; Holman, 2006), a “plethodon-like” plethodontid reported from Texas by Parmley (1989) and an unidentified plethodontid from the Pipe Creek Sinkhole of Indiana (Farlow et al., 2001). Ambystomatidae has perhaps the best representation

Figure 1.1. Representative of the amphibian Order Caudata (salamanders), *Notophthalmus viridescens* (the Eastern Newt) in the juvenile red 'eft' stage. Photograph taken by Blaine W. Schubert.

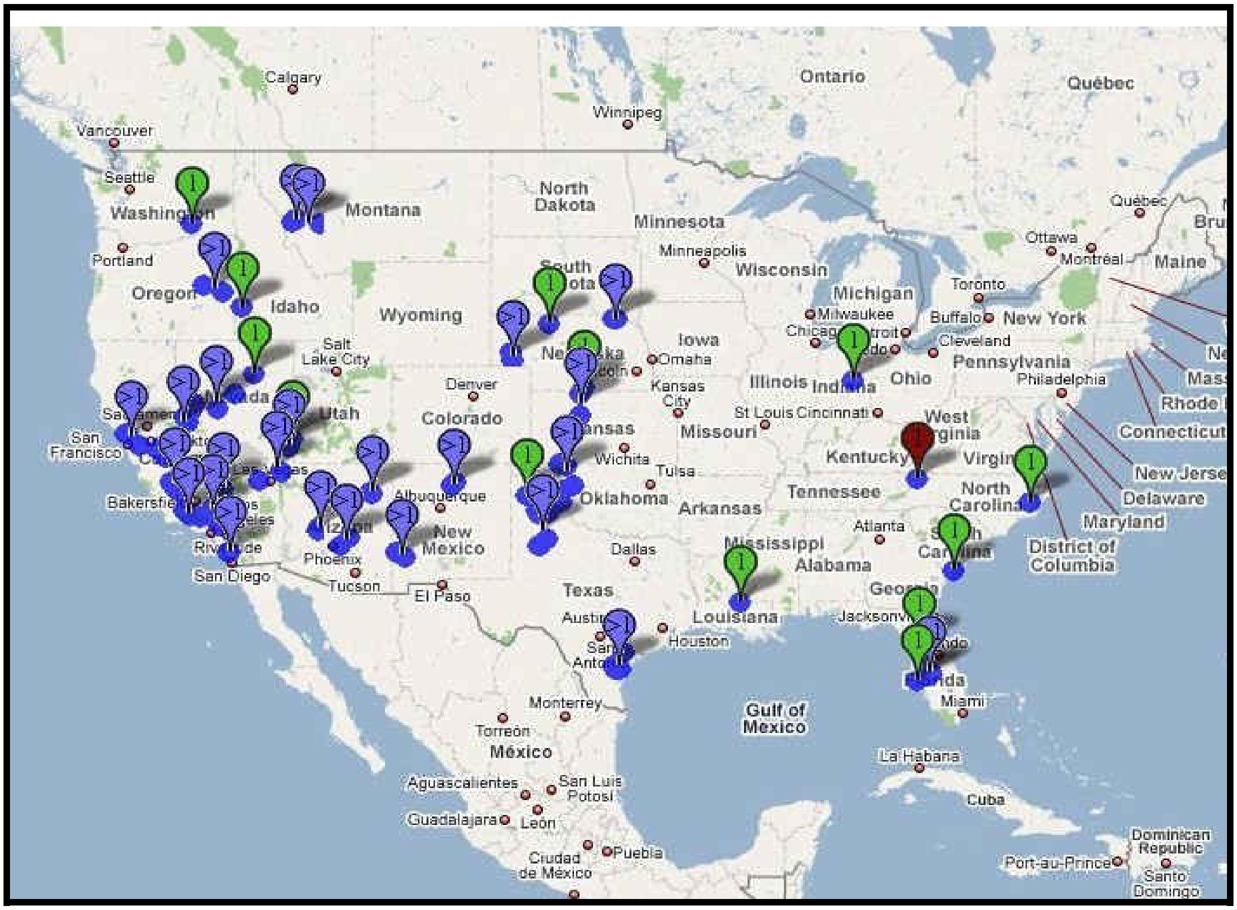

Figure 1.2. Map of the United States showing where Mio-Pliocene aged fossil sites have been recovered: green call-outs represent areas with one site; blue call-outs represent areas with multiple sites; the red call-out is the Gray Fossil Site (GFS). GFS is the only Mio-Pliocene aged site known from the Appalachian region, and one of the few terrestrial, non-marine sites in eastern North America. Modified from Carrasco et al. (2005).

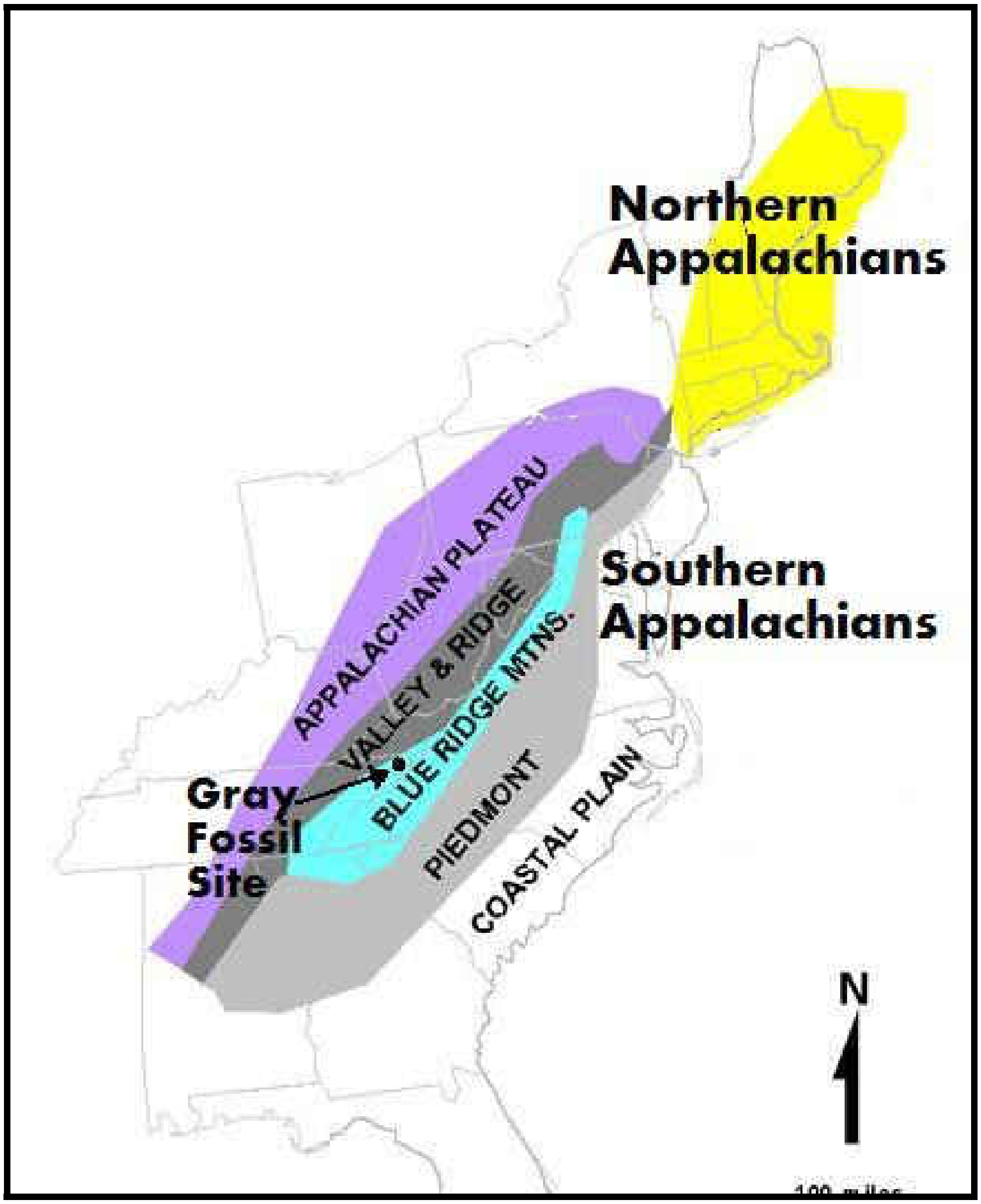

Figure 1.3. Map of the Appalachian Mountains region. Modified from the U.S. Geological Survey.

in the Mio-Pliocene record, with several species of *Ambystoma* being found in Kansas and Texas (Holman, 2006). The Salamandridae are represented by trackways in Kansas; and the Batrachosauroididae has its last representative in California (Naylor, 1981; Holman, 2006).

Focusing on fossil salamander vertebrae for identification purposes is complex: on one hand they have features that easily distinguish them as belonging to salamanders; but on the other hand due to their simplicity and an overlap in general characters between clades identification below family level can be very difficult. Another surprising obstacle to unequivocal identification comes from past descriptive works that include vague (and very often completely subjective) descriptions, lack of adequate illustrations, and a lack of discrete characters, but that are accepted as seminal and canonical in the field. There is also the tendency (especially in Pleistocene and Holocene sites) to identify and describe fossil species based on modern species endemic to the area, which leads to a circular argument when these biased identifications are used to illustrate past biogeographic ranges (e.g. Holman, 1958, 1959, 1966, 1977, and 1982). Current workers are moving towards finding discrete characters and working with large comparative collections rather than depending on the circular reasoning provided by modern biogeographic and seminal description biases (e.g. Olori and Bell, 2007).

No overarching character keys exist for identifying salamander vertebrae to genus and species, though several reports (e.g. Tihen, 1958; Wake, 1963; Edwards, 1976; Estes, 1981; Miller and Van Devender, unpublished; Holman, 2006; and Olori and Bell, unpublished) present a good basis for outlining discrete, non-overlapping characters useful for identification purposes. Tihen (1958) notes several characters useful for distinguishing ambystomatid salamanders (in which he included the families Ambystomatidae, Dicamptodontidae, and Rhyacotritonidae) from other groups and each other, and characters including vertebral ratios that are helpful in identifying *Ambystoma* vertebrae to subfamily. Wake (1963) gives a comparative osteological account of three closely related plethodontids (i.e. *Aneides*, *Ensatina*, and *Plethodon*), providing characters that help to distinguish the three from one another. Edwards (1976) dealt with the placement pattern and number of spinal nerve foramina in the vertebral column of all salamander families and its bearing on phylogeny; in the process providing a single character that allows for various levels of identification. Estes (1981) and Holman (2006) both provide broad characters that allow for identification to the generic level and present helpful illustrations, but neither present these characters in a comprehensive format that could be used as a key for identification. Miller and Van Devender (unpublished) provides an account of the majority of North American salamander taxa in key format (though unfortunately not illustrated) that, used in conjunction with a large comparative collection, is perhaps the best tool for identifying fossil salamander trunk vertebrae to genus level. Olori and Bell (unpublished) tackled overlapping characters between several families and provide several discrete, non-overlapping characters that are helpful for identification to family and generic levels.

The GFS is rich in fossil salamander remains (predominantly isolated vertebrae) that can be identified to family and generic levels; preliminary sorting of specimens recovered from screening over the past four years has identified more than 2,000 skeletal elements as salamanders from three families (Ambystomatidae, Plethodontidae, and Salamandridae). This abundance of identifiable salamander fossils provides the opportunity to elucidate on the evolutionary and biogeographic histories of salamander clades in a region that is well known as a center of modern salamander diversity. Fossils specimens from the GFS provide a unique opportunity to examine a Mio-Pliocene sinkhole deposit in the southern Appalachians and add to the extent of the fossil record for salamanders in southeastern North America. The primary objectives of this thesis are to: 1) identify a subset of the salamander fossils from the GFS to family, subfamily, and genus by comparing them with skeletons of modern species and published characters, 2) draw paleoecological inferences about the GFS (beyond those of Schubert, 2006, and Schubert and Wallace, 2006) based on physiological parameters and habitat preference of modern analogs through phylogenetic bracketing, and 3) further elucidate the evolutionary and biogeographic history of salamander clades in southeastern North America.

CHAPTER 2

FIRST MIO-PLIOCENE SALAMANDER FAUNA FROM SOUTHERN APPALACHIA

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Abstract

Continued screening efforts at the Gray Fossil Site, Washington County, Tennessee, have yielded a unique and diverse salamander fauna for the southern Appalachian Mio-Pliocene. This fauna includes at least five taxa (*Ambsytoma* sp.; *Plethodon*-type and Spelerpinae-type plethodontids, *Desmognathus* sp., and *Notophthalmus* sp.) from three families (Ambystomatidae, Plethodontidae, and Salamandridae respectively) present in the area today and supporting the woodland-pond interpretation of the site. All specimens represent the earliest record of their families in the Appalachian Mountains (and the earliest record of Plethodontidae and Ambystomatidae east of the Mississippi River), with the *Notophthalmus* sp. vertebrae being the only Mio-Pliocene body fossil known for the Salamandridae in North America. The *Desmognathus* sp. specimens may help shed light on the evolutionary origins of the genus *Desmognathus*, which purportedly has its roots in this region during the Mio-Pliocene. The GFS salamander fauna is predominated by plethodontids. Competition is inferred by the presence of several similarly large-sized taxa and is invoked to explain the presence of neotenic individuals in an otherwise amicable terrestrial environment.

Three salamander families are reported from the Mio-Pliocene Gray Fossil Site (GFS) of Washington County, northeastern Tennessee (Figure 2.1): Ambystomatidae, Plethodontidae, and Salamandridae. Ambystomatidae have perhaps the best fossil record in the Mio-Pliocene of the three families present at the GFS, with vertebrae of *Ambystoma* cf. *A. minshalli* from the Coffee Ranch Local Fauna of Texas (Parmley, 1989) and *A. kansense*, a neotenic form, from Edson Quarry, Kansas (Holman, 2006). The Mio-Pliocene fossil record of the Plethodontidae is nearly exclusive to California with tracks and vertebrae from *Batrachoseps* found in the Pinhole Tuff, Mehrten Formation (Clark, 1985; Holman, 2006) and an otic bone of *Aneides lugubris* from Turlock Site 5 (Clark, 1985); up to this point only two records of the family have been reported east of the Rockies, a single 'plethodon-like' trunk vertebra from Coffee Ranch, Texas (Parmley, 1989) and unidentified plethodontid material from the Pipe Creek Sinkhole of Indiana (Farlow et al., 2001). The family Salamandridae has no skeletal fossil record in the Mio-Pliocene, instead being represented by a trackway in Kansas referred to *Taricha* sp. (Holman, 2006).

GFS is the only Mio-Pliocene fossil site in the Appalachian region, providing a unique look at a diverse salamander fauna in an upland environment. The fossil site covers an area roughly 1.8-2.0 ha by up to 39 m thick of sediments (Nave et al., 2005). The site is a package of finely laminated clays, silts, and fine sands intermixed with isolated gravel lenses as the result of a small lake or pond filling a paleosinkhole within the Cambrian/Ordovician Knox Group Dolostone (Wallace and Wang, 2004; Shunk et al., 2006; DeSantis and Wallace, 2008; Hulbert et al., 2009). Weathering and erosion of the bedrock subsequent to the infilling has generated a reversed topography, leaving the fossil site as a high point (Wallace and Wang, 2004; Shunk et al., 2006). Overlapping stratigraphic ranges of the rhinoceros *Teleoceras* and the shortfaced bear *Plionarctos* found associated at the GFS constrains the age of the assemblage to between 4.5 and 7 Myr (Wallace and Wang, 2004). The bulk of the herpetofauna at GFS (including alligators, natricine snakes, aquatic testudines, anurans, and salamanders) reflect a 'pond' environment (Schubert, 2006; Schubert and Wallace, 2006). As noted by Wallace and Wang (2004) and Jiang and Liu (2008), abundant plant macrofossils from *Quercus* (Oak) and *Carya* (Hickory), in the form of leaves, acorns and nuts, and isotope work by DeSantis and Wallace (2008) indicate a forest surrounded the 'pond'.

Fossils from the GFS provide a unique opportunity to examine a Mio-Pliocene sinkhole deposit in the southern Appalachians and add to the extent of the fossil record for salamanders in southeastern North America. The primary objectives of this report are to 1) identify a subset of the salamander fossils from the GFS to family, subfamily or type, and genus by comparing them with skeletons of modern species from all extant families and published characters, 2) draw paleoecological inferences about the GFS (beyond those of Schubert,2006, and Schubert and Wallace, 2006) based on physiological parameters and habitat preference of modern analogs through phylogenetic bracketing, and 3) further elucidate the evolutionary and biogeographic history of salamander clades in southeastern North America.

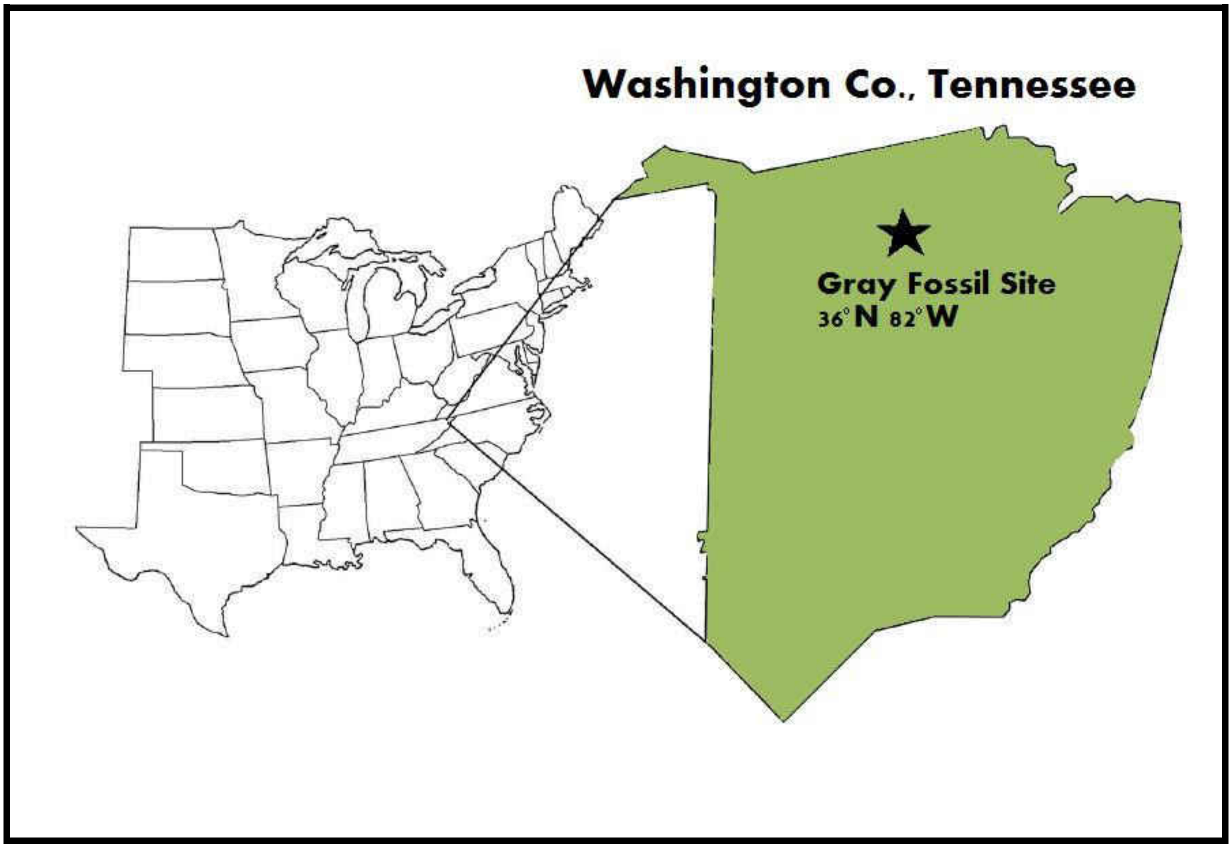

Figure 2.1. Location of the Gray Fossil Site, northeastern Tennessee. Modified from DeSantis and Wallace (2008).

Materials and Methods

Fossil Collection and Identification

Vertebrate microfossil remains were collected by water screening matrix from the various test pits at the GFS using 1.7 mm mesh box screens. Screened residue was then picked under a dissecting microscope and remains were sorted by class and order. Preliminary identification of the salamander fossils was done by comparison under a light microscope with modern specimens housed and/or on loan at East Tennessee State University.

Identification of fossil salamander skeletal elements is complicated by the overall simplicity of salamander bones in general, phylogenetic and ontogenetic variation, and similarity between unrelated taxa. The age of the GFS (4.5 to 7 Ma) makes species attribution based on vertebrae seemingly implausible along with lack of confidence in identification below family, so fossil taxa are only identified to the level of genus where possible. Because vertebrae are the most numerous element in the skeleton and the most represented fossil element at the GFS, special attention was given to vertebral anatomy. Following the osteological scheme of Duellman and Trueb (1994), the salamander vertebral column consists of five differentiated regions: cervical (consisting of the atlas), trunk (containing a variable number of vertebrae from 10 to 60 depending on genus or species), sacrum (consisting of one sacral vertebra), caudosacral (consisting of two to four vertebrae), and caudal region (with a variable number of vertebrae from 20 to more than 100) (Figure 2.2). GFS salamander vertebrae were identified by comparing the fossil material with modern specimens from all families and literature on various taxa. Comparative specimens used for this analysis were from the Carnegie Museum of Natural History (CMNH), University of California Museum of Vertebrate Zoology (UCMVZ), New Jersey State Museum (NJSM), Appalachian State University (ASU), and from the personal

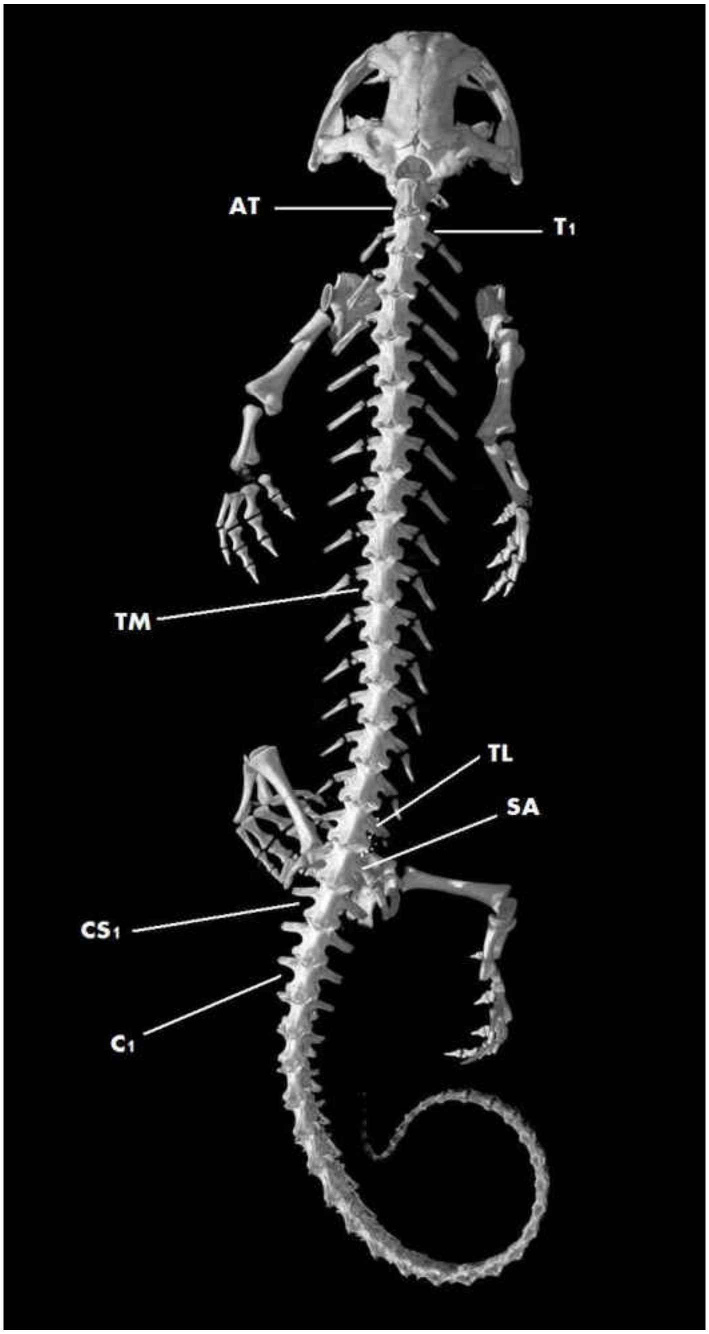

Figure 2.2. Skeleton of *Ambystoma tigrinum* illustrating the divisions of the vertebral column: AT (atlas), T1 (first trunk vertebra), TM (mid-trunk vertebra), TL (posteriormost trunk vertebra), SA (sacrum), CS1 (first caudosacral), and C1 (first caudal). Modified from DigiMorph Staff (2008).

collections of Blaine W. Schubert, Jim I. Mead, Dennis C. Parmley, and R. Wayne Van Devender.

After preliminary examination of both modern comparative and fossil specimens, and literature regarding vertebral characters of the extinct family Batrachosauroididae, two major assumptions were made in regards to identification of the GFS material: 1) GFS specimens represent living families (i.e. no Batrachosauroididae) , and 2) the presence of spinal nerve foramina posterior to the transverse processes in trunk vertebrae is a character present in only four living salamander families: Ambystomatidae, Plethodontidae, Salamandridae, and Sirenidae. Thus the presence of these foramina in all the examined GFS trunk vertebrae limits identification to the aforementioned families. Of the above mentioned modern families, the Sirenidae were excluded from further identification purposes based on the complex structure of their vertebrae including the diagnostic V-shaped posterior expansion of the neural arch, alar processes forming V-shaped structures in lateral view, and sharp hemal keels. Where identifications are made to 'type' (as in the case of the plethodontids) further identification is discussed but left for future work due to a lack of confidence in generic level characters.

Data Analysis

Screening of fossil rich sediment at the GFS is an ongoing process so specimens were selectively sampled for analysis. Though this selectivity may not be entirely reflective of taxon abundance, it was perhaps the best practice in light of the preliminary nature of the excavation. Relative abundances of fossil salamander taxa are represented in three ways, the number of identified elements for the taxon (NIE), minimum number of individuals for the taxon (MNI), and in a pie chart (see Discussion) comparing very rough percentages of taxa abundance in the random sample. MNI is a conservative estimate of the minimum number of individuals of a taxon that are necessary to account for the number of skeletal elements in the identified sample. As an example, if 2 atlantes, 1 middle trunk, and 3 sacral vertebrae were found for a taxon, the MNI would be 3 (because salamanders have only one sacral vertebra and one atlas).

Results

Systematic Accounts

A total of 181 pre-caudal vertebrae identified from a random sample represent at least five salamander genera. Vertebral identification methods are emphasized here because vertebrae are the most abundant salamander elements from the site (and the only elements identifiable beyond ordinal level). Each fossil genus account includes a breakdown of the identified vertebrae by position in the vertebral column, NIE, MNI, and remarks regarding the identification of these elements. Anatomical terminology (see Glossary in Appendix) follows that of Duellman and Trueb (1994), Miller (1992), and Holman (2006). Classification used was that of Duellman and Trueb (1994), Larson et al. (2006), and Chippindale et al. (2004).

Order Caudata Oppel, 1811
Suborder Salamandroidea Noble, 1931
Family Ambystomatidae Hallowell, 1856
Genus *Ambystoma* Tschudi, 1838
Mole Salamanders

Reference Specimens: 2 *Ambystoma maculatum* (JIM 0836 and 3139), 1 neotenic *A. tigrinum nebulosum* (FB 31), 2 neotenic *A. tigrinum* (FB 55 and DCP 453), and 5 *A. tigrinum* (FB 826, FB 816, JIM 0841, DCP 556, NJSM B434), 1 larval *A. tigrinum* (FB 60).

The family Ambystomatidae is comprised of one genus, *Ambystoma*, and approximately 31 species (Larson et al., 2006: Wells, 2007). Ambystomatids are restricted to North America, being found from Alaska to Mexico, and most are moderately large terrestrial salamanders with lungs (Petranka, 1998). Terrestrial species are generally pond breeders, laying their eggs in winter or early spring (Petranka, 1998; Wells, 2007), then residing in leaf litter or burrows not far from the breeding pond for the remainder of the year (Petranka, 1998). Neoteny (the retention of larval features, like external gills, into sexual maturity) is expressed in several species and populations of ambystomatids that are wholly aquatic; this is especially common at high altitude or in arid regions where the terrestrial environment would be inhospitable to metamorphosed adults (Wells, 2007).

Vertebral Morphology:

General features of the ambystomatid vertebrae are illustrated in Figure 2.3. Vertebrae of *Ambystoma* are amphicoelous (Figure 2.3) and have spinal nerve foramina posterior to the transverse processes in all vertebrae except the first trunk vertebra (T1) (Edwards, 1976; Miller, 1992). The atlas has paired atlantal cotyles, and a non-faceted odontoid process (see Figure 2.4). T1 has widely separated and robust transverse processes, whereas the other trunk vertebrae have less robust transverse processes where the diapophyses and parapophyses are fused for the majority of their lengths (see Figure 2.5). As noted by Tihen (1958) and Miller (1992), the anterior trunk vertebrae (T1-T3) are proportionally shorter and broader, with steeper neural arches and proportionally larger neural canals. Other trunk vertebrae have lower neural arches and are longer (see Figure 2.6). In general the hyperapophyses are high and have a vertical posterior face (Olori and Bell, 2007). The last trunk vertebra (TL) has completely fused transverse processes like the two caudosacral (CS) vertebrae (see figure 2.5), except that the transverse processes are directed dorsally rather than ventrally (Miller, 1992). For both the TL and CS the transverse processes are acuminate (i.e. come to a point). In general *Ambystoma* tend to have inter-prezygapophyseal neural arch margins that are V-shaped or that are deeply convex, except for the T1 which just as often has a linear inter-prezygapophyseal neural arch margin.

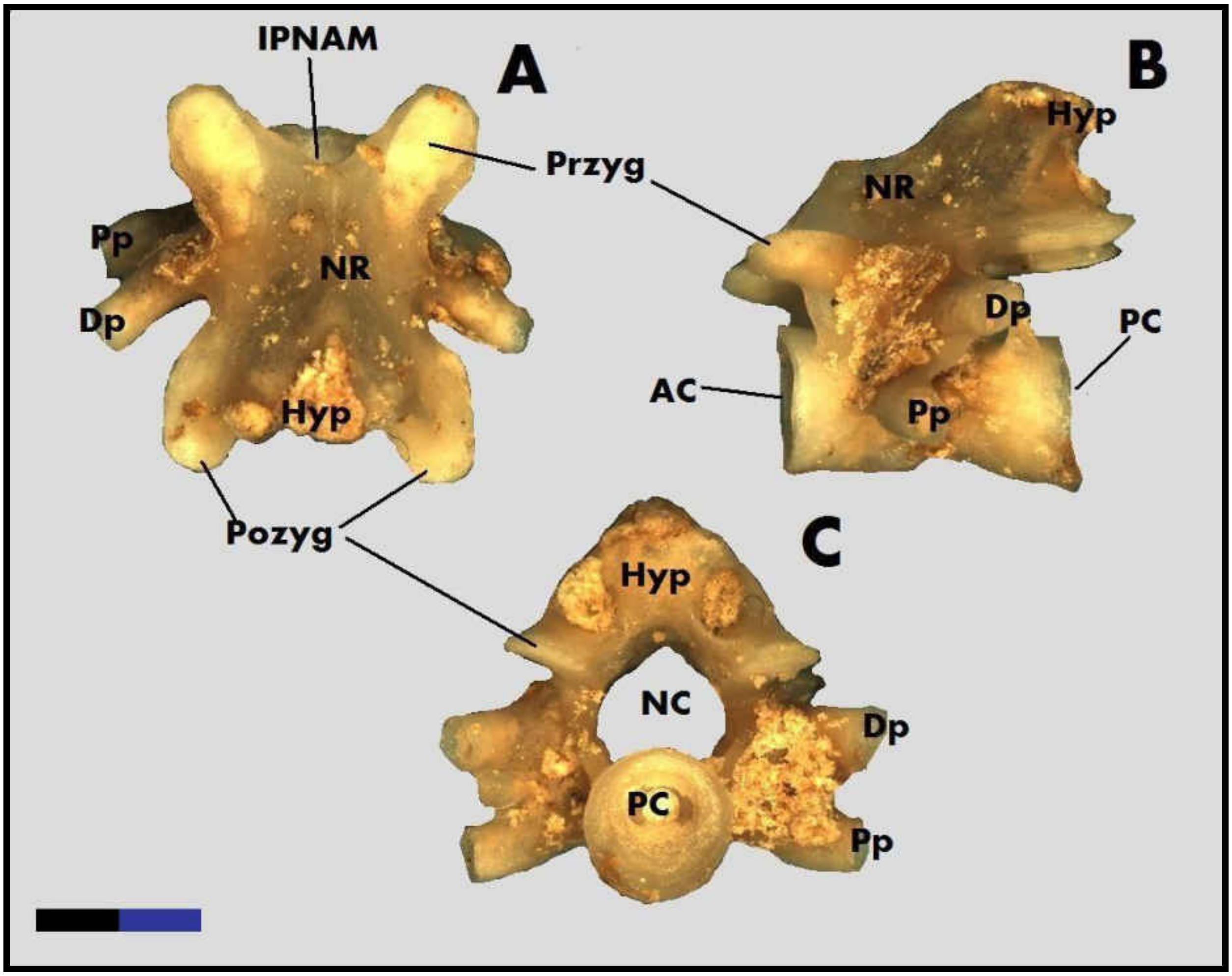

Figure 2.3. Reference (FB 826) *Ambystoma tigrinum* second trunk vertebra in A) dorsal, B) left lateral, and C) posterior views illustrating features noted in description: AC = anterior cotyle, Dp = diapophysis, Hyp = hyperapophysis, IPNAM = inter-prezygapophyseal neural arch margin, NC = neural canal, NR = neural ridge, PC = posterior cotyle, Pp = parapophysis, Przyg = prezygapophyses, Pozyg = postzygapophyses. Scale bar is 2 mm.

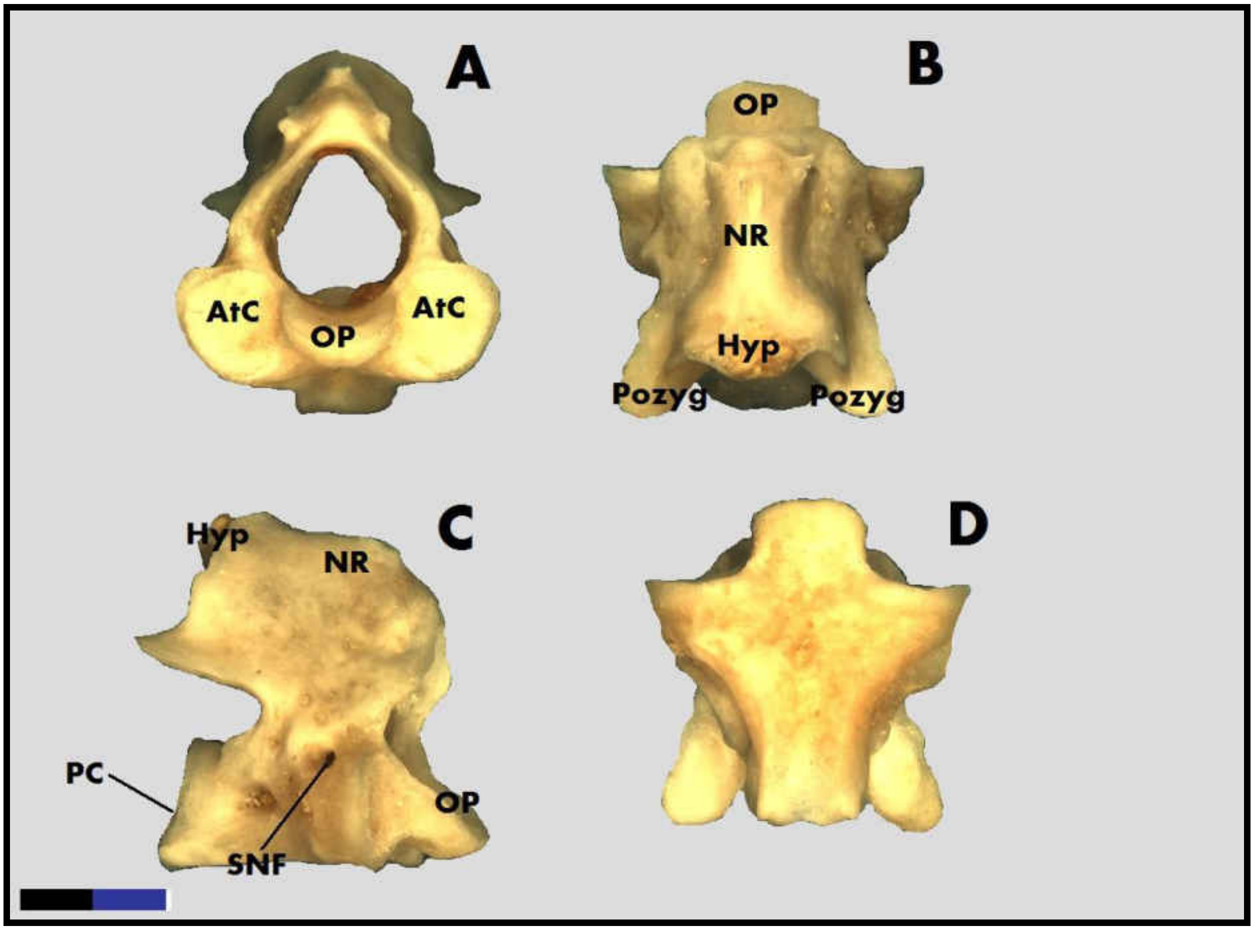

Figure 2.4. Reference (FB 826) *Ambystoma tigrinum* atlas in A) anterior, B) dorsal, C) right lateral, and D) ventral views illustrating features described: AtC = atlantal cotyle, Hyp = hyperapophysis, NR= neural ridge, OP = odontoid process, PC = posterior cotyle, Pozyg = postzygapophyses, SNF = spinal nerve foramina. Scale bar is 2 mm.

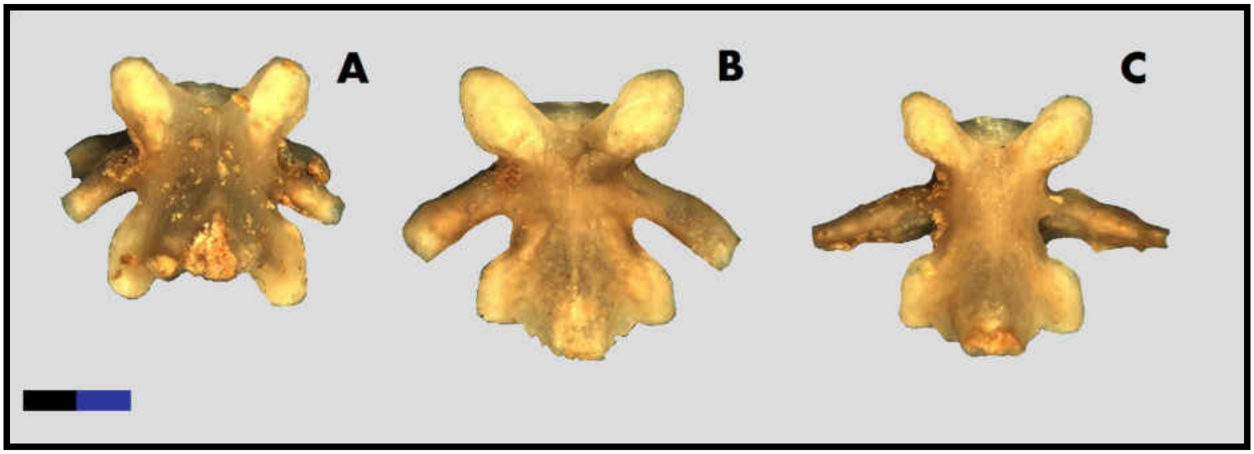

Figure 2.5. Reference (FB 826) *Ambystoma tigrinum* A) anterior trunk vertebra, B) sacral vertebra, and C) caudosacral vertebra in dorsal views. Scale bar is 2 mm.

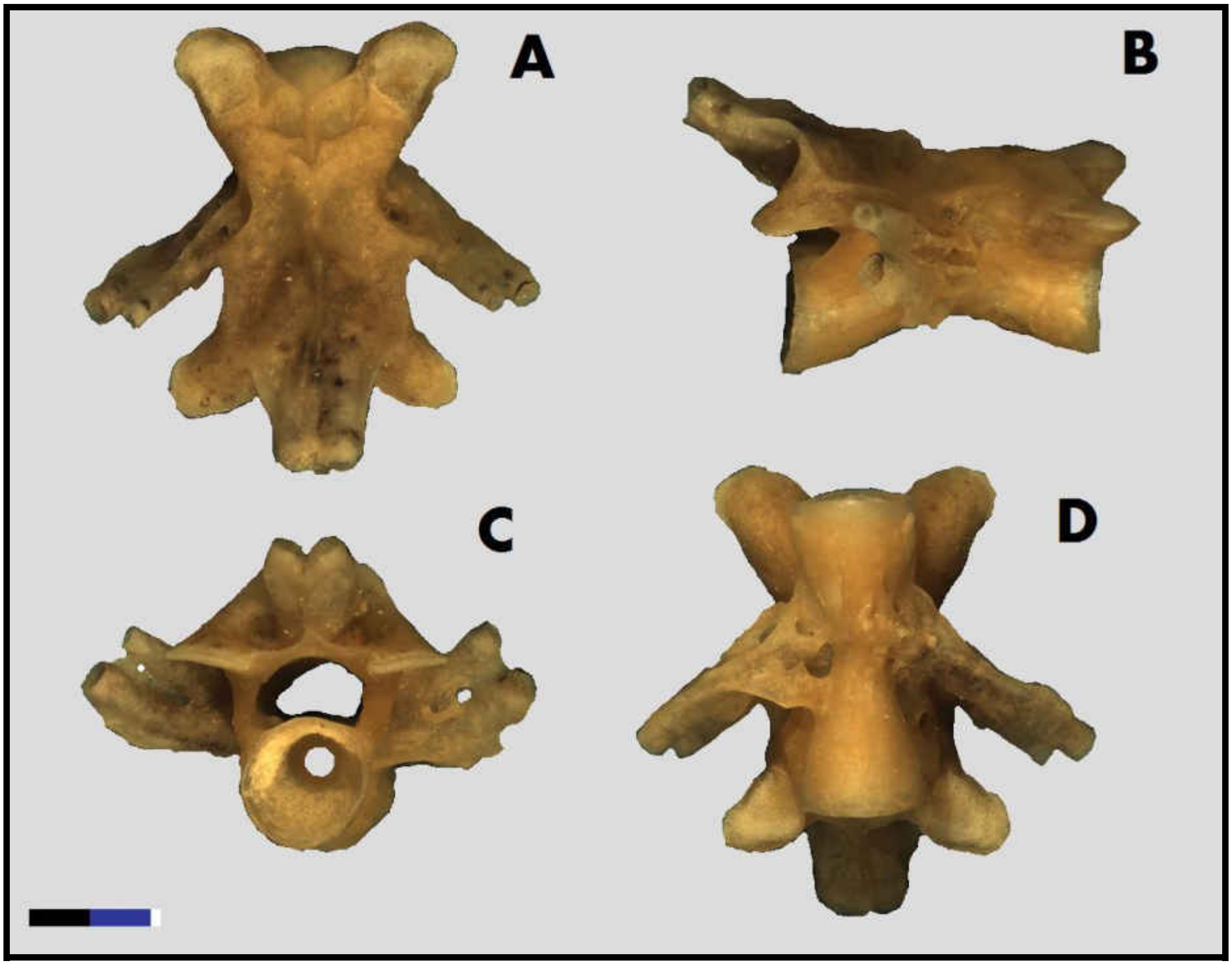

Figure 2.6. Reference (FB 31) neotenic *Ambystoma tigrinum nebulosum* trunk vertebra in A) dorsal, B) right lateral, C) posterior, and D) ventral views. Note elongate hyperapophyses and continuous notochordal canal distinctive of neotenic ambystomatids. Scale bar is 2 mm.

Ambystoma sp.

Fossil material: 3 atlantes (ETMNH 3852, 3853, 3854); 1 first trunk vertebra (ETMNH 3857); 1 second or third trunk vertebra (ETMNH 3859); 25 mid-trunk vertebrae (ETMNH 1863, 4938, 4939, 4940, 4942, 4935, 4936, 4917, 4918, 3858, 3861, 3862, 1876-1881); 3 last trunk vertebrae (ETMNH 1882, 3856, and 4941); 5 sacral vertebrae (ETMNH 3855, 4924, 4928, 1872, 1873); 1 caudosacral vertebra (ETMNH 3860). NIE = 38 and MNI = 3 (based on atlantes) or 8 (see remarks on Sacral vertebrae).

Remarks:

Robust amphicoelous vertebrae with robust transverse processes, V-shaped inter-prezygapophyseal neural arch margins, and notably elevated posterior portion of the neural arch are here referred to *Ambystoma* sp.

ATLAS (AT). Atlantes are large and robust, with non-faceted odontoid processes widely separating the atlantal cotyles. Atlantal cotyles are roughly circular and in all fossil specimens are more ventrally located than in modern *Ambystoma tigrinum* (compare Figures 2.4A and 2.7A), in that respect resembling modern *A. maculatum*. Posterior cotyles are circular. Neural canals are circular and bordered by a thick neural arch. The neural arch elevates posteriorly nearly 45 degrees meeting a tall atlantal hyperapophysis (see Figure 2.7C); the postzygapophyseal articular facets are teardrop-shaped and slightly elevated posteriorly. Spinal nerve foramina are situated postero-laterally and slightly dorsally to the mid-line of the atlantal cotyles (see Figure 2.7C).

FIRST TRUNK VERTEBRA (T1). Posterior and anterior cotyles are circular. Neural canal is large and constricted dorsally, the canal openings appearing nearly triangular (see Figure 2.8A). The anterior half of the neural arch is horizontal (i.e. flat) with a slightly raised neural crest, whereas the posterior half is rising 45 degrees to meet a broad hyperapophysis that does not extend beyond the posterior margin of the postzygapophyses. The inter-prezygapophyseal neural arch margin is linear. Postzygapophyseal articular facets are oval-shaped and horizontally oriented; the prezygapophyseal articular facets are also oval-shaped but are slightly elevated posteriorly. Transverse processes are robust, the parapophyses originating in front of the middle of the centrum, the diapophyses in the middle of the neural arch wall; both processes project posteriorly. Large vascular foramina are present in the base of the parapophyses; there are no spinal nerve foramina.

SECOND OR THIRD TRUNK VERTEBRAE (T2 or T3). Posterior and anterior cotyles are circular. The neural canal is roughly circular. The anterior half of the neural arch is horizontal with a slightly raised neural crest, the posterior half of the neural arch rising slightly more than 45 degrees to meet a broad (and perhaps bifurcated) hyperapophysis. The hyperapophysis does not extend beyond the posterior margin of the postzygapophyses. The inter-prezygapophyseal neural arch margin is V-shaped. The postzygapophyseal and prezygapophyseal articular facets are oval-shaped and horizontally oriented. The transverse processes are robust and project posteriorly; the parapophyses originating in the middle of the centrum and the diapophyses in the middle of the neural arch wall (see Figure 2.10D). The diapophyses are ventrally constricted (see Figure 2.10F). There is a single spinal nerve foramina posterior to the diapophyses; vascular foramina are present.

MID-TRUNK VERTEBRAE (TM). These vertebrae are amphicoelous, and many have anterior basapophyses. Posterior and anterior cotyles are circular. The neural canal is roughly circular and precedes to become more flattened in the more posterior vertebrae. The anterior half of the neural arches are horizontal with a slightly raised neural crest, whereas the posterior half is rising around 45 degrees to meet broad, slightly bifurcated hyperapophyses. The inter-prezygapophyseal neural arch margins are generally V-shaped (see Figures 2.9 and 2.10). The postzygapophyseal and prezygapophyseal articular facets are oval-shaped and horizontally oriented. The transverse processes are long and less robust and posteriorly projected. There is a single spinal nerve foramina present posterior to the diapophyses, and vascular foramina are present. Roughly 50 percent of the mid-trunk vertebrae have open notochordal canals (see Figure 2.9), a feature generally expressed in neotenic (Figure 2.6) individuals (Tihen, 1942; Holman, 1975; Holman, 2006). The presence of neotenic individuals at the GFS is counter to the interpreted absence of neoteny put forward by Boardman et al. (2008).

POSTERIORMOST TRUNK VERTEBRAE (TL). This vertebra is amphicoelous, elongate and has a low profile. The posterior and anterior cotyles are roughly circular and slightly ventrally flattened. The neural canal is flattened and the neural arch is relatively flat with a nearly obsolete neural ridge. The posterior half of the neural arch rising less than 45 degrees to meet the hyperapophysis (see Figure 2.11). The inter-prezygapophyseal neural arch margins are generally V-shaped. The postzygapophyseal articular facets are circular and prezygapophyseal articular facets are oval-shaped, both are horizontally oriented. The transverse processes (which originate at the middle of the vertebra) are slender, fused, and postero-dorsally projected; the diapophyses are acuminate. Single spinal nerve foramina are present posterior to the diapophyses, vascular foramina are also present.

SACRAL (SA). These vertebra are amphicoelous, elongate and have a lower profile than most of the other vertebrae (except TL) that precede it. Posterior and anterior cotyles are circular. The neural canal is flattened and the neural arch is relatively flat with a nearly obsolete neural ridge. The posterior half of the neural arch is rising less than 45 degrees to meet the hyperapophysis, that extends beyond the posterior margin of the postzygapophyses (see Figure 2.12). The inter-prezygapophyseal neural arch margins are generally V-shaped. The postzygapophyseal articular facets are circular and prezygapophyseal articular facets are oval-shaped, both are horizontally oriented. The transverse processes (which originate at the middle of the vertebra) are long, completely fused, becoming more robust at their distal end, and are posteriorly projected. The sacral vertebra has large spinal nerve formina posterior to the diapophyses. Several sacral vertebrae may be representative of small- to medium-sized neotenic individuals of *Ambsytoma* sp. (see Figure 2.12), these vertebrae have a considerably lower profile, neural canals and arches are flattened, neural ridges are obsolete to non-existent, and hyperapophyses are flattened and extend well beyond the posterior extent of the postzygapophyses. The possibility that these sacral vertebrae may represent a neotenic plethodontid cannot be overlooked, but until more neotenic plethodontids can be examined, these specimens will remain tentatively in *Ambystoma* sp.

CAUDOSACRAL VERTEBRA (CS). This vertebra is amphicoelous and is similar in character to the last trunk vertebra except in that the transverse processes are postero-ventrally projected.

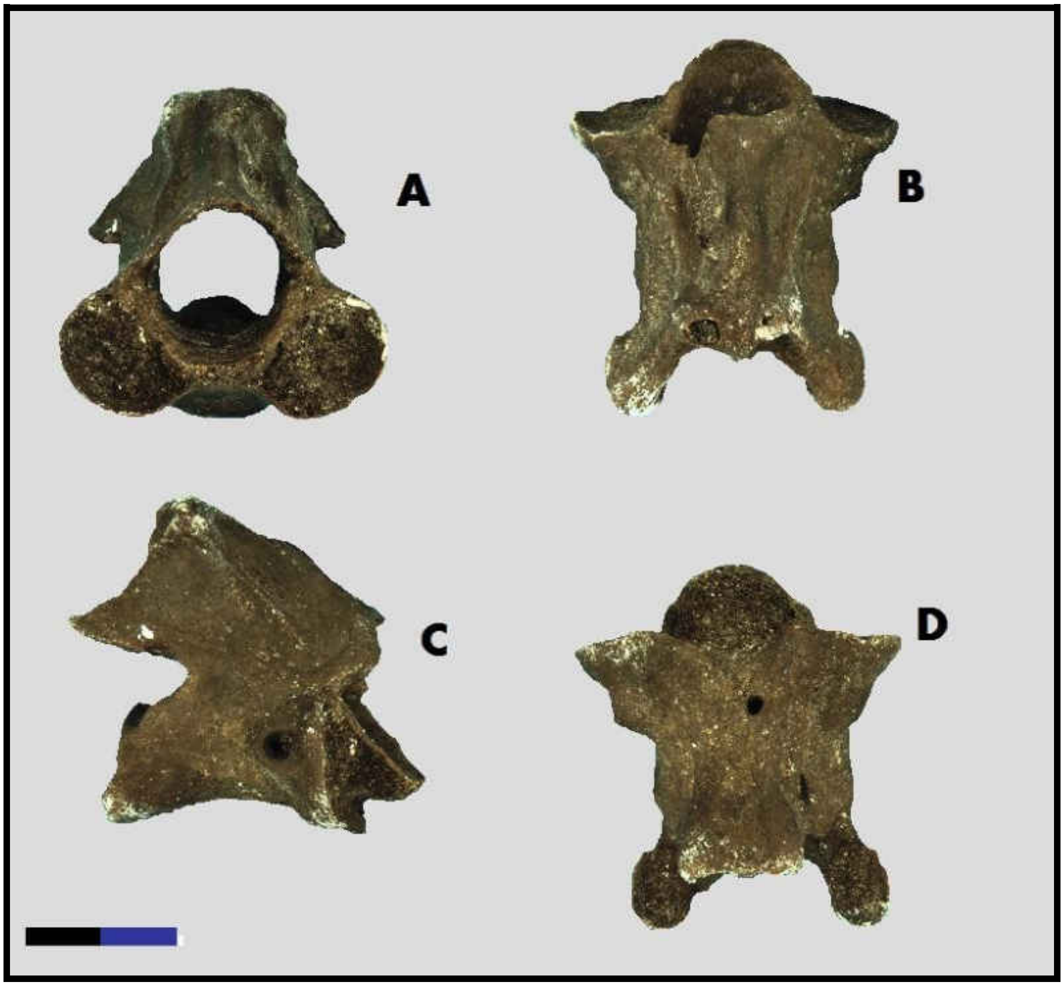

Figure 2.7. ETMNH 3852 *Ambystoma* sp. atlas in A) anterior, B) dorsal, C) right lateral, and D) ventral views. Scale bar is 2 mm.

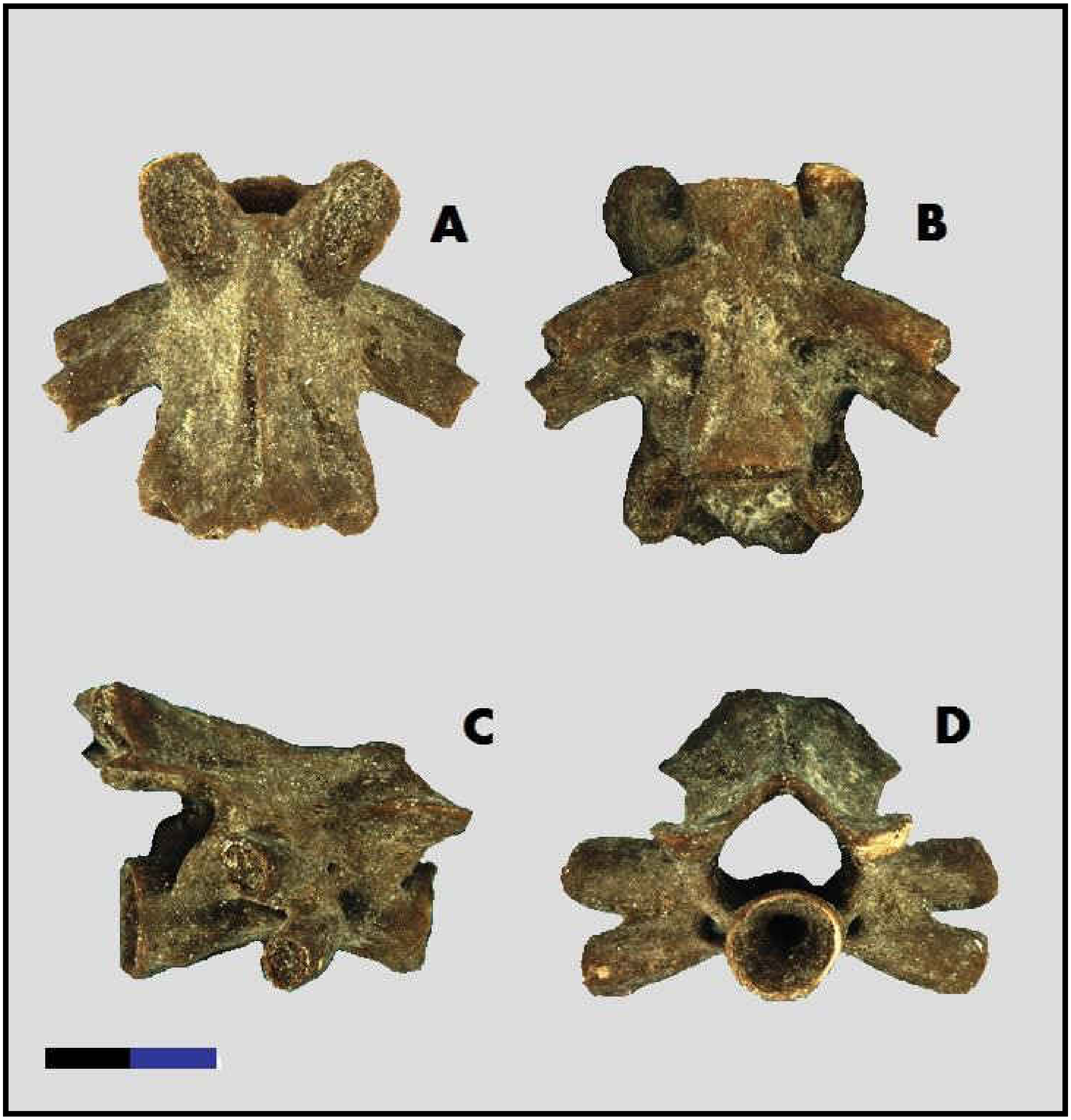

Figure 2.8. ETMNH 3857 *Ambystoma* sp. first trunk vertebra (T1) in A) dorsal, B) ventral, C) right lateral, and D) anterior views. Scale bar is 2 mm.

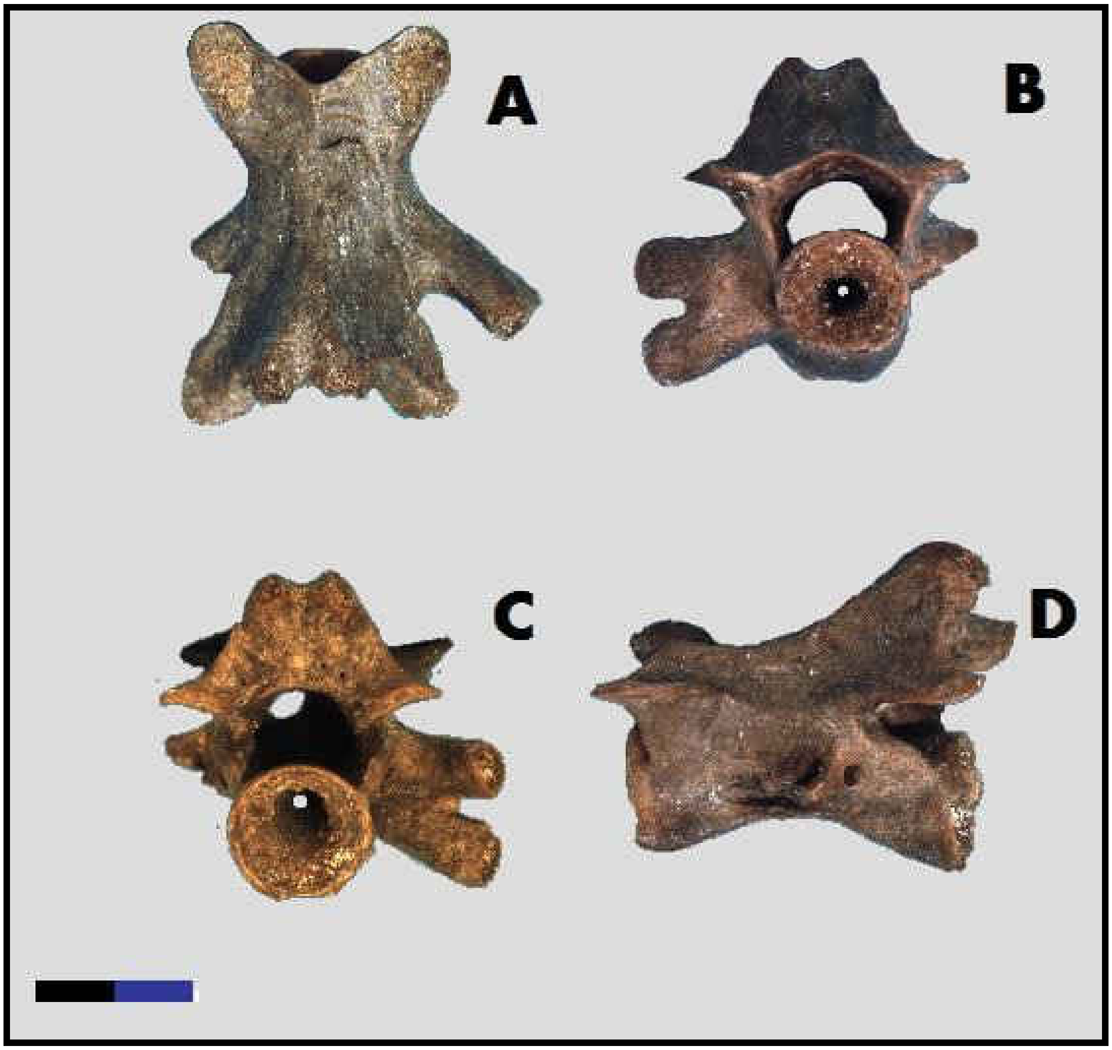

Figure 2.9. ETMNH 4917 *Ambystoma* sp. trunk vertebra exhibiting neoteny in A) dorsal, B) anterior, C) posterior, and D) left lateral views. Scale bar is 2 mm.

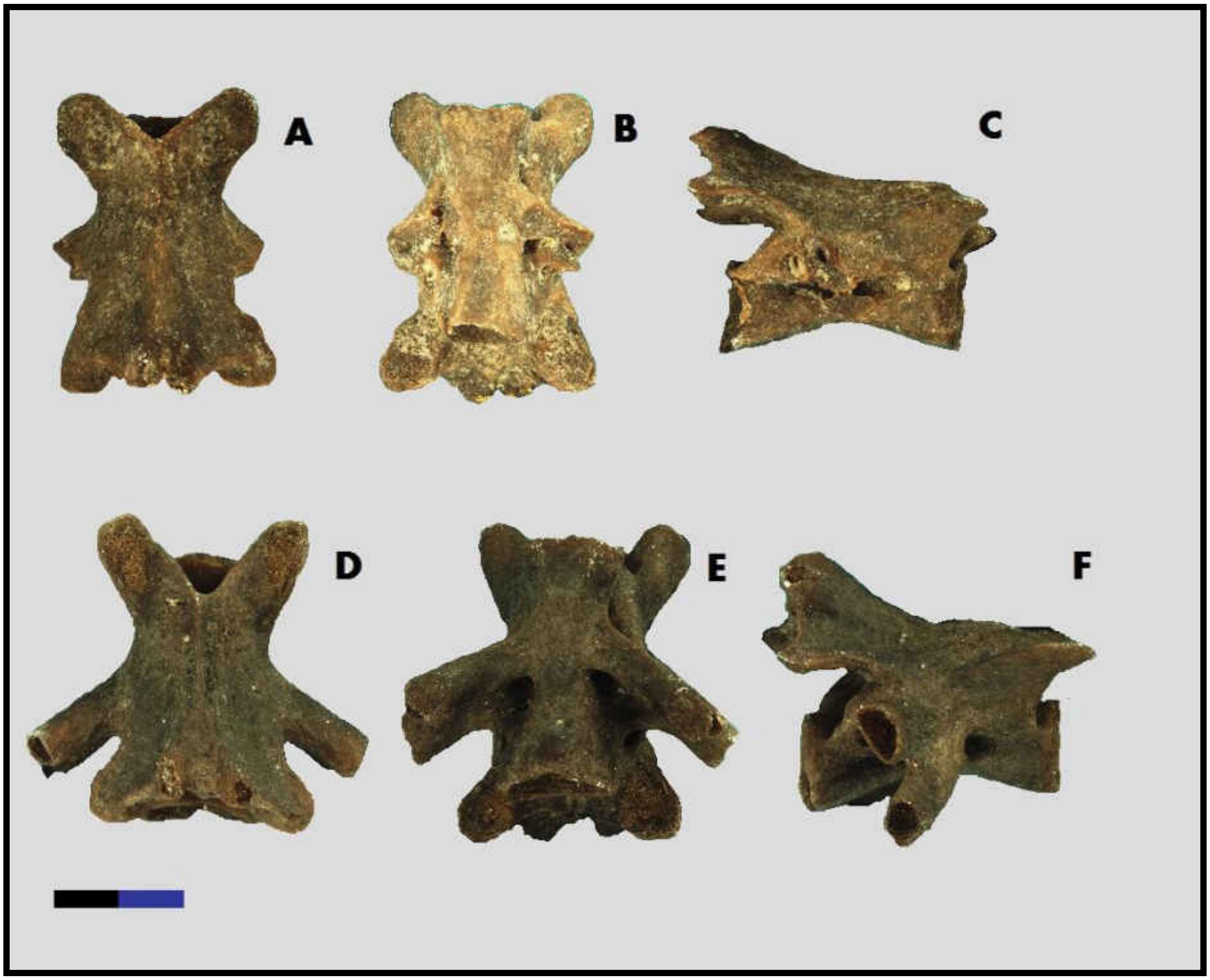

Figure 2.10. ETMNH 3858 *Ambystoma* sp. anterior trunk vertebra in A) dorsal, B) ventral, and C) right lateral views; ETMNH 3859 *Ambystoma* sp. anterior trunk vertebra (T2 or T3) in D) dorsal, E) ventral, and F) right lateral views. Scale bar is 2 mm.

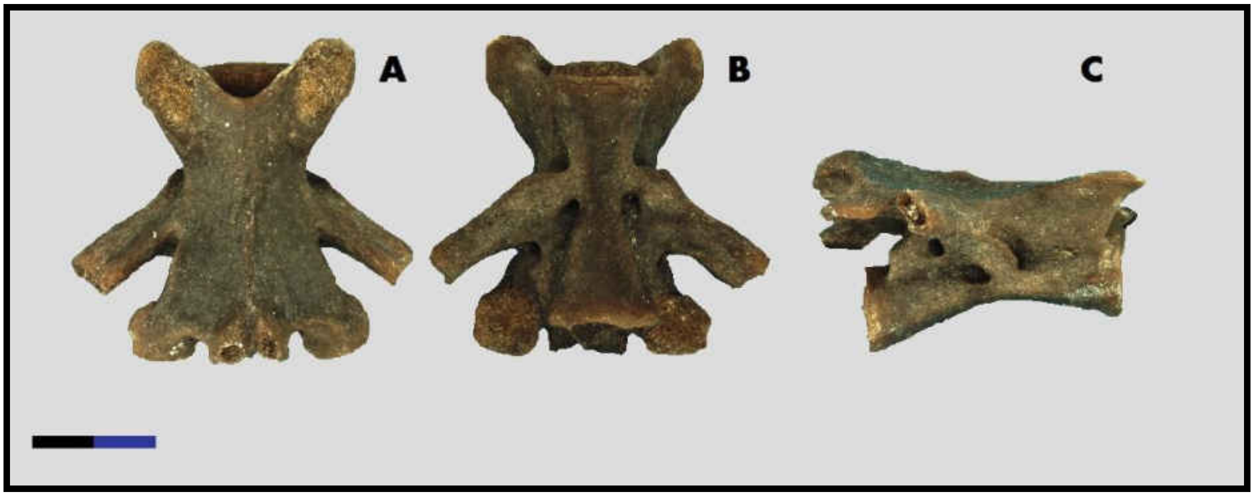

Figure 2.11. ETMNH 3856 *Ambystoma* sp. last trunk vertebra (TL) in A) dorsal, B) ventral, and C) right lateral views. Scale bar is 2 mm.

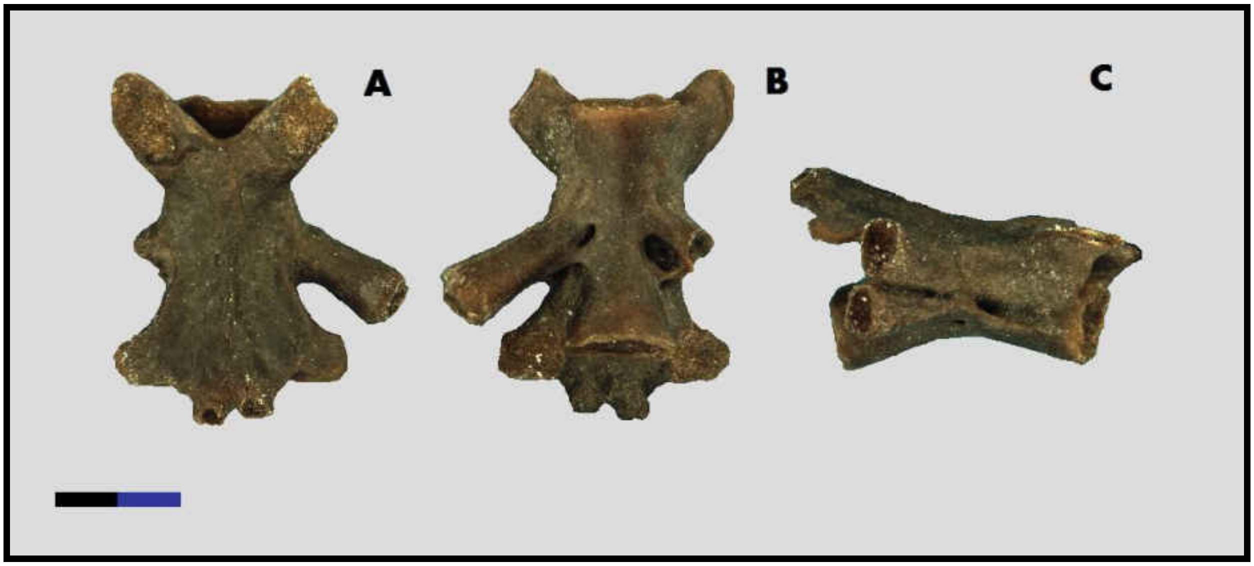

Figure 2.12. ETMNH 3855 *Ambystoma* sp. sacral vertebra (SA) in A) dorsal, B) ventral, and C) right lateral views. Scale bar is 2 mm.

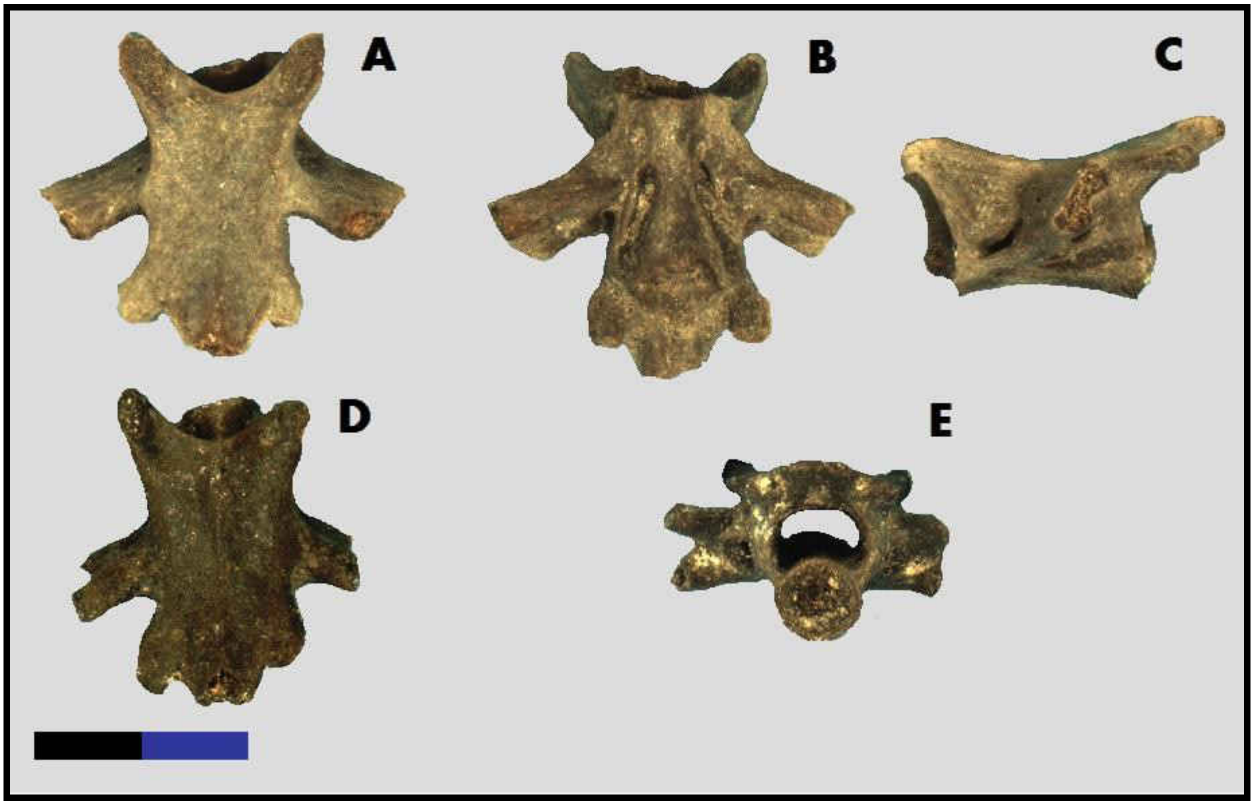

Figure 2.13. ETMNH 4924 ?neotenic *Ambystoma* sp. sacral vertebra in A) dorsal, B) ventral, and C) left lateral views; ETMNH 4928 ?neotenic *Ambystoma* sp. sacral vertebra in D) dorsal and E) posterior views. Scale bar is 2 mm.

Family Plethodontidae Gray, 1850

Lungless Salamanders

Reference Specimens: 1 *Eurycea longicauda* (ASU 17370), 1 *Eurycea lucifuga* (BWS 0014), 1 *Eurycea guttolineata* (DCP 3694), 2 *Aneides lugubris* (ASU 15317 and FB 3403), 1 *Pseudotriton montanus* (ASU 18722), 1 *Desmognathus brimleyorum* (ASU 15332), 1 *D. monticola* (JIM 0808), 1 *D. quadramaculatus* (JIM 0811), 1 *Ensatina eschscholtzii* (JIM 0771), 2 *Gyrinophilus porphyriticus* (CMNH 138925 and 33975), 1 *Hydromantes shastae* (UCMVZ 228772), 1 *Stereochilus marginatus* (RWV 1792), 1 *Plethodon glutinosus* (BWS 0016), 1 *Pseudoeurycea belli* (TRVD).

The salamander family Plethodontidae is the largest and most diverse of the Order Caudata, distributed throughout the Americas and with sparse populations in southern Europe and eastern Asia (Duellman and Trueb, 1994; Min et al., 2005). The family is broken up into four subfamilies: Plethodontinae, Spelerpinae, Hemidactylinae, and Bolitoglossinae (Chippindale et al., 2004). Though the family has adapted to a wide array of habitats (arboreal, aquatic, terrestrial, and fossorial) and in general produce direct developing young, they are still restricted to moist environments because they do not have lungs and rely on cutaneous respiration (Wells, 2007).

Vertebral Morphology:

Features used for description of plethodontid vertebrae are illustrated in Figure 2.14. Plethodontid atlantes have odontoid processes with paired articular facets (see Figure 2.15), unlike in *Ambystoma* (Miller, 1992). Vertebrae of plethodontids are amphicoelous (though in some genera they are opisthocoelous) and have spinal nerve foramina posterior to the transverse processes in all vertebrae except the first trunk vertebra (T1), which has spinal nerve foramina anterior to the transverse processes (Miller, 1992). Second trunk vertebra (T2) has spinal nerve foramina both posterior and anterior to the transverse processes (Edwards, 1976; Miller, 1992). With regards to the rest of the trunk vertebrae the first three trunk vertebrae (T1-T3) have transverse processes that are more posteriorly directed, have proportionally shorter centra, and have larger neural canals (Miller, 1992). The remaining trunk vertebrae, except the last trunk vertebra (TL), are very similar to one another (see figures 2.16 and 2.17). The TL has diapophyses that are reduced, acuminate (Miller, 1992) and either have a single very large spinal nerve foramen (as in members of the subfamily Plethodontinae) or two spinal nerve foramina (as in most members of the subfamily Spelerpinae). The sacrum has more robust transverse processes that are united for much of their length (Miller, 1992). Species in which tail autotomy has evolved generally have three or four caudoscrals (e.g. *Hemidacytlium scutatum* has three), whereas those that have not developed this escape strategy only have two caudosacrals (e.g. *Desmognathus monticola*). The caudosacrals have transverse processes that are completely fused and acuminate, and often have alar processes (Miller, 1992). In general plethodontids tend to have linear to slightly concave inter-prezygapophyseal neural arch margins (see figures 2.16 and 2.17), a character used by Olori and Bell (unpublished) to distinguish plethodontids from some of the more gracile ambystomatids.

Subfamily Plethodontinae Gray, 1850

The plethodontid subfamily Plethodontinae (*sensu* Chippingdale et al. [2004]; Macey [2005]; Min et al. [2005]) is comprised of *Aneides*, *Ensatina*, *Hydromantes*, *Karsenia*, and *Plethodon* + *Desmognathus*.

Plethodon-type

Fossil material: 5 atlantes (ETMNH 1864, 3847, 4920, 4921), 3 first trunk vertebrae (ETMNH 4922, 4923, 4926), 5 second trunk vertebrae (ETMNH 1865, 4943, 3850, 3851, 3846), 1 third trunk vertebra (ETMNH 7260), 62 mid-trunk vertebrae (ETMNH 7239-7241, 7243, 7244, 7246-7249, 7251, 7252, 7254-7259, 7261-7274, 7276, 7277, 4932-4934, 4929, 4925, 4927, 3863, 1866,1859, 1862), 3 last trunk vertebrae (ETMNH 7242, 7245, 7275), 3 caudosacral vertebrae (ETMNH 1861, 7271, 7253). NIE = 82 and MNI = 5 (based on the number of atlantes).

Remarks:

Gracile, amphicoelous vertebrae with linear to slightly concave inter-prezygapophyseal neural arch margins are here referred to *Plethodon*-type.

ATLAS (AT). The *Plethodon*-type atlantes come in two forms: Type A and Type B (see figure 2.18). Both atlantal morphotypes have odontoid processes with paired articular facets (which clearly distinguish both from the atlantes of ambystomatids). Type A has circular atlantal cotyles which are laterally placed and the robust form has sub-circular cotyles which are more ventrally placed. Type A has foramina on the ventral surface of the centrum, whereas Type B does not. The neural arch of Type B is thick and tall, and the neural canal is sub-circular. Type A has a thinner, lower neural arch in profile. The posterior cotyle in both morphotypes are circular. Neither has well-preserved postzygapophyses, so little can be said about their general shape or orientation.

FIRST TRUNK VERTEBRA (T1). These trunk vertebrae are amphicoelous. The posterior and anterior cotyles are circular, with the posterior cotyle being more ventrally placed. The neural canal is large, with the walls of the neural arch expanding laterally beyond the centrum. A neural ridge is moderately- to well-developed in the center of the neural arch and the hyperapophyses are gently raised and do not extend beyond the posterior margin of the postzygapophyses. The prezygapophyseal articular facets are elongate, projecting beyond the anterior neural arch margin for nearly half their length (see figure 2.19A). These articular facets are also distinctly raised laterally and the inter-prezygapophyseal neural arch margins are linear. The postzygapophyseal articular facets are also elongate. The transverse processes are small and narrow, with the parapophyses being anterior to the diapophyses. A single spinal nerve foramina is present anterior to the diapophyses.

SECOND TRUNK VERTEBRA (T2). These trunk vertebrae are amphicoelous and in general have the same features as the T1, except that they possess spinal nerve foramina both anterior and posterior to the diapophyses.

THIRD TRUNK VERTEBRA (T3). This vertebra is amphicoelous and appears to generally share the features of the first two trunk vertebrae except that is has a single spinal nerve foramina posterior to the diapophyses.

MID-TRUNK VERTEBRAE (TM). These vertebrae are amphicoelous, narrow and appear in two morphotypes: Type A and Type B. The anterior and posterior cotyles are circular, with the posterior cotyle being slightly larger and placed more ventrally. The neural canal is wider than tall and the neural arch is generally flat with a distinct, but medially restricted neural ridge (see figure 2.19D). The posterior portion of the neural arch rises only slightly, ending in paired hyperapophyses that generally do not extend beyond the posterior margin of the postzygapophyses. The prezygapophyseal and postzygapophyseal articular facets are generally narrow, widening anteriorly, and are slightly laterally inclined. In general the transverse processes are posteriorly projected and relatively short, with the diapophyses being smaller in diameter and placed more posteriorly than the parapophyses. The diapophyses and parapophyses are often connected by a web of bone for part of their lengths. Some of these vertebrae have basapophyses, but most do not. All mid-trunk vertebrae have a single spinal nerve foramina posterior to the diapophyses, and vascular foramina are generally present in the basal portion of the parapophyses.

POSTERIORMOST TRUNK VERTEBRAE (TL). These vertebrae are amphicoelous and in general share the same features as the mid-trunk vertebrae except the diapophyses are acuminate, and the parapophyses are connected to the centrum by weakly developed ventral alar processes.

CAUDOSACRAL VERTEBRAE (CS). These vertebrae are amphicoelous and share most of the features of the last vertebrae except that their transverse processes are completely fused, acuminate, and connected to the centrum by ventral alar processes.

Vertebrae here referred to *Plethodon*-type are more like *Plethodon* and *Ensatina* than they are to non-plethodontine plethodontids.

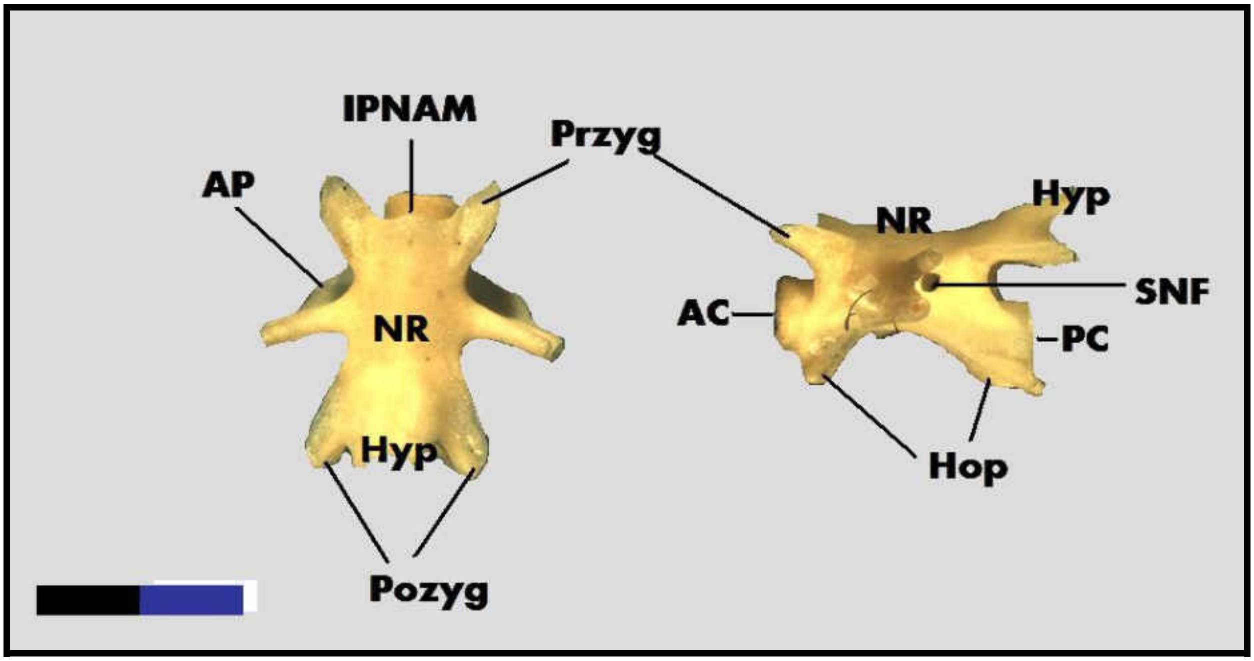

Figure 2.14. Generalized plethodontid reference trunk vertebra (JIM 0808, *Desmognathus monticola*) in dorsal and left lateral views illustrating features noted in descriptions: AC = anterior cotyle, AP = alar process, Hop = hypophyses, Hyp = hyperapophyses, IPNAM = inter-prezygapophyseal neural arch margin, NR = neural ridge, PC = posterior cotyle, Pozyg = postzygapophyses, Przyg = prezygapophyses, SNF = spinal nerve foramina. Scale bar is 2 mm.

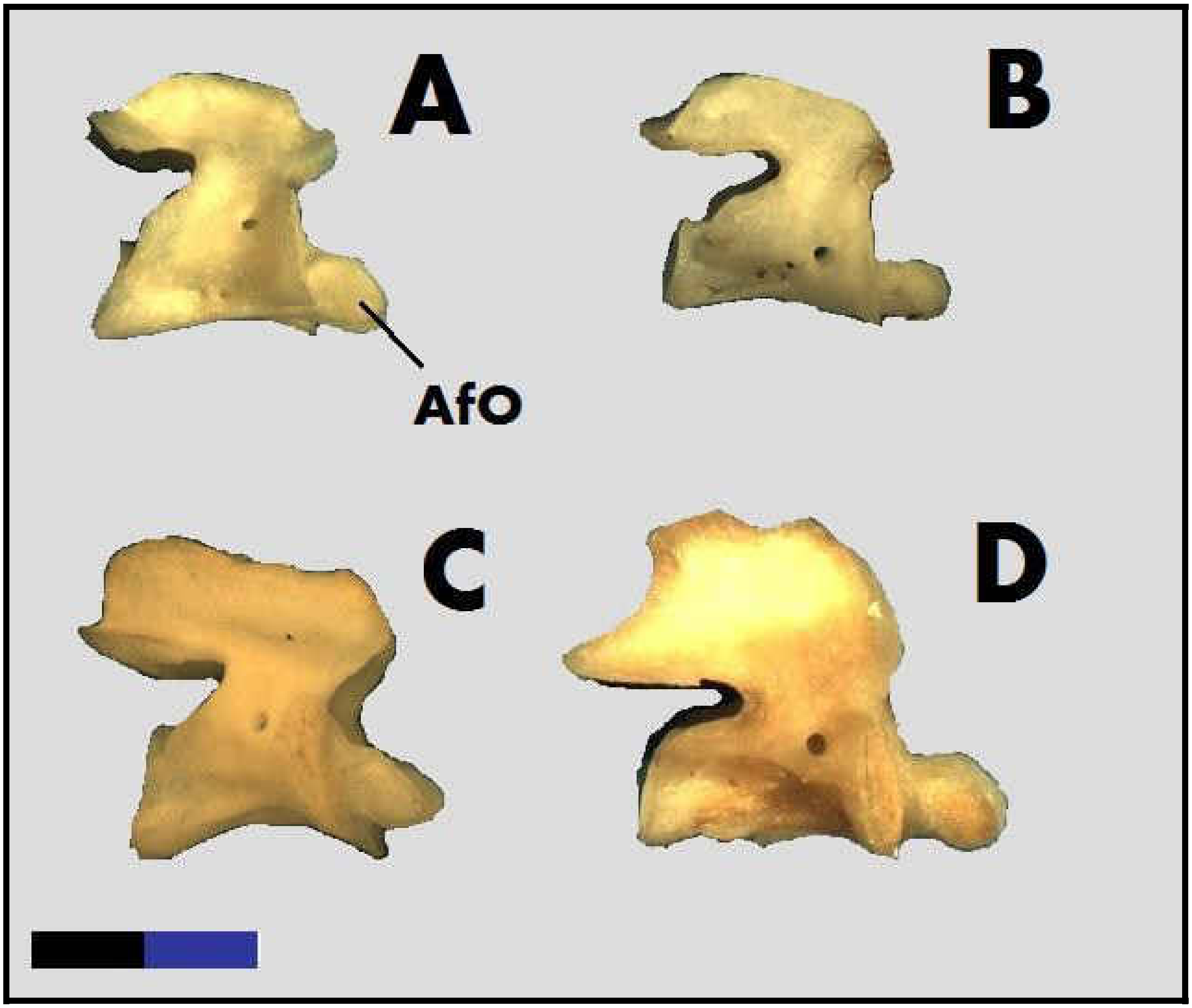

Figure 2.15. Reference plethodontid atlantes: A) *Ensatina eschscholtzii* (JIM 771), B) *Eurycea lucifuga* (BWS 0014), C) *Gyrinophilus porphyriticus* (CMNH 138925), D) *Pseudoeurycea belli* (TRVD) in right lateral views. Note articular facets on the odontoid processes (AfO) in all reference specimens. Scale bar is 2 mm.

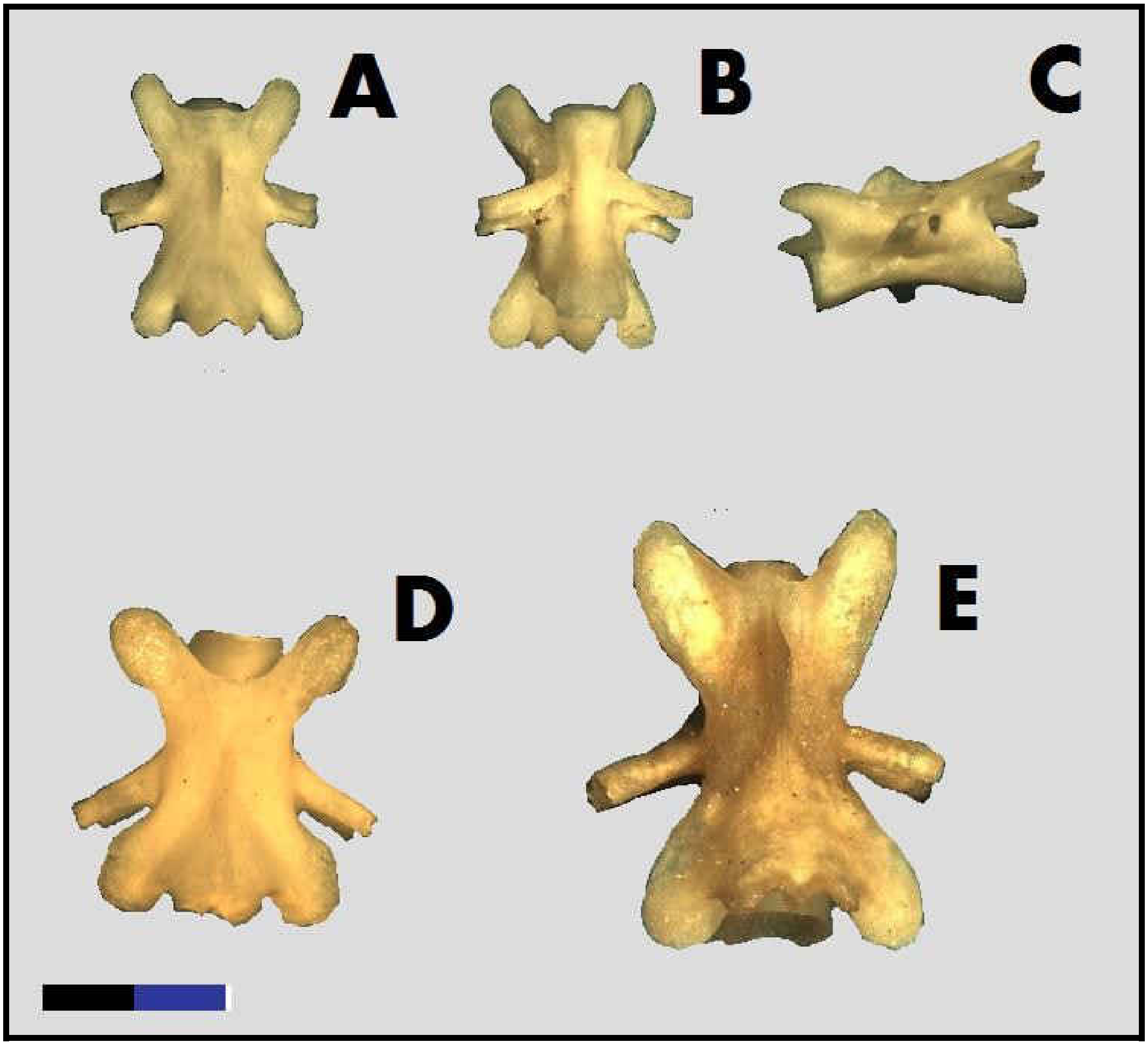

Figure 2.16. Reference plethodontid trunk vertebrae: (BWS 0016) *Plethodon glutinosus* trunk vertebra in A) dorsal, B) ventral, and C) left lateral views; D) (CMNH 138925) *Gyrinophilus porphyriticus* and E) (TRVD) *Pseudoeurycea belli* in dorsal views. Scale bar is 2 mm.

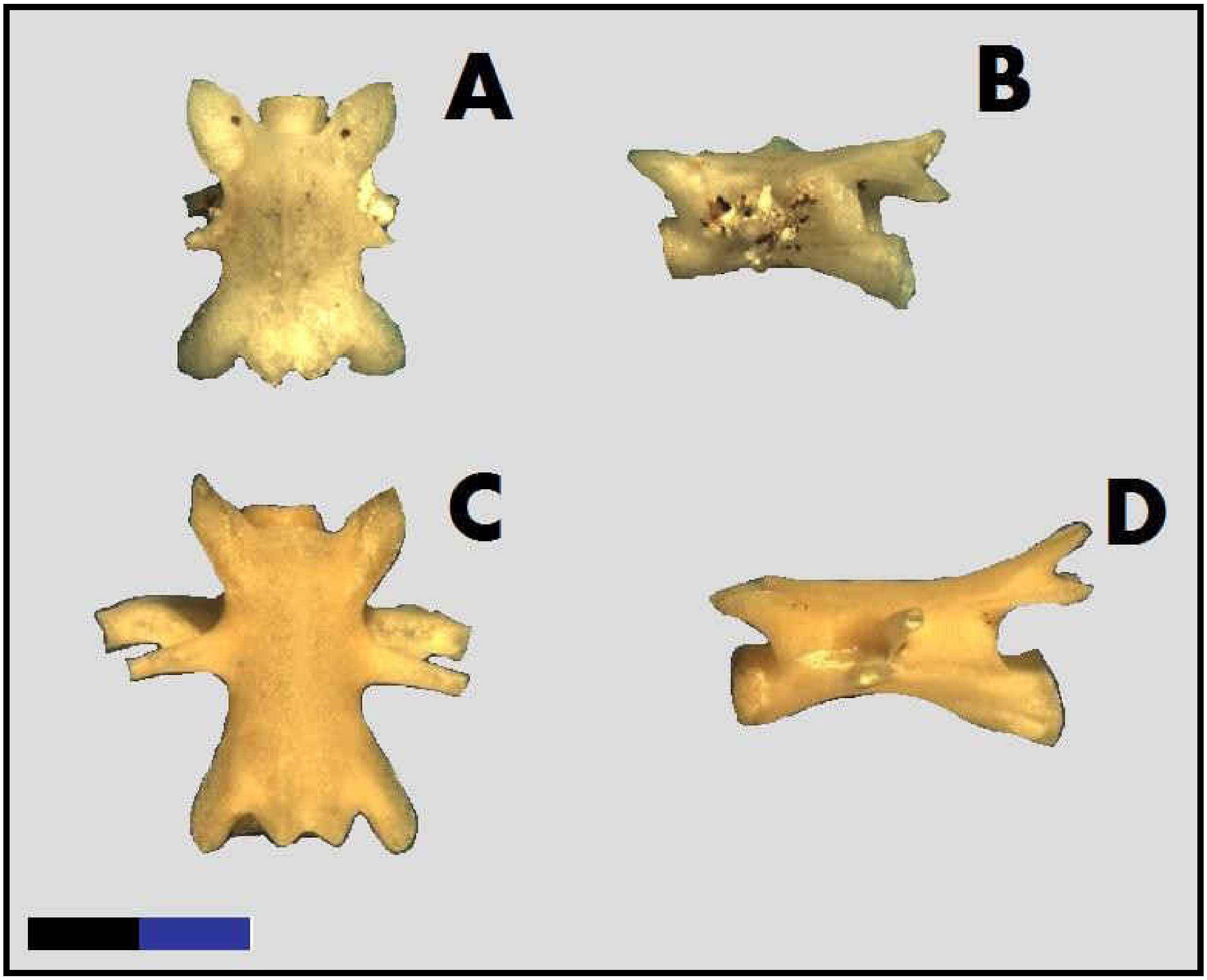

Figure 2.17. Reference plethodontid trunk vertebrae: (BWS 0014) *Eurycea lucifuga* in A) dorsal and B) left lateral views; (JIM 0808) *Desmognathus monticola* in C) dorsal and D) left lateral views. Scale bar is 2 mm.

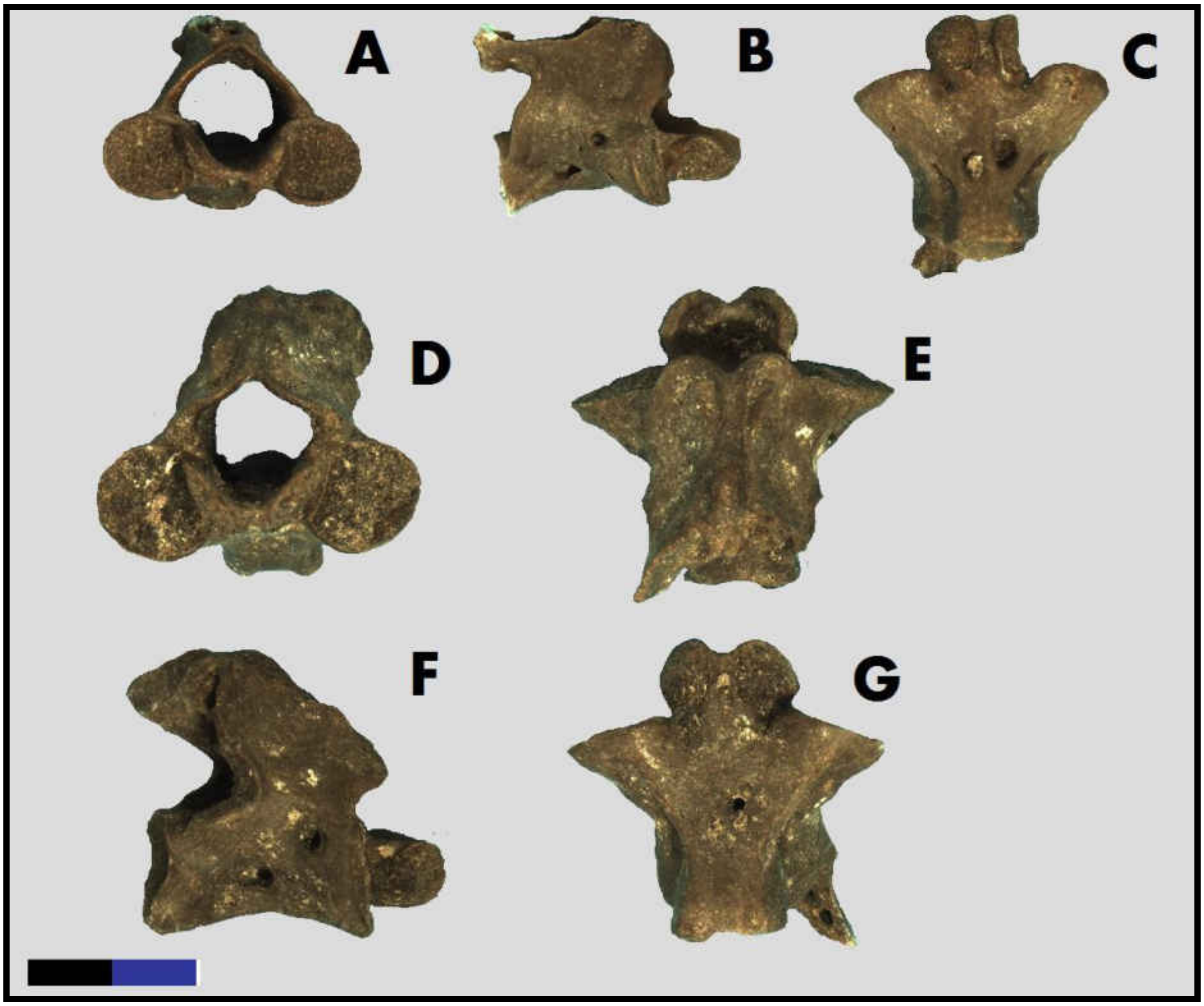

Figure 2.18. ETMNH 3847 *Plethodon*-type plethodontid Type A atlas in A) anterior, B) right lateral, and C) ventral views; ETMNH 4920 *Plethodon*-type plethodontid Type B atlas in D) anterior, E) dorsal, F) right lateral, and G) ventral views. Scale bar is 2 mm.

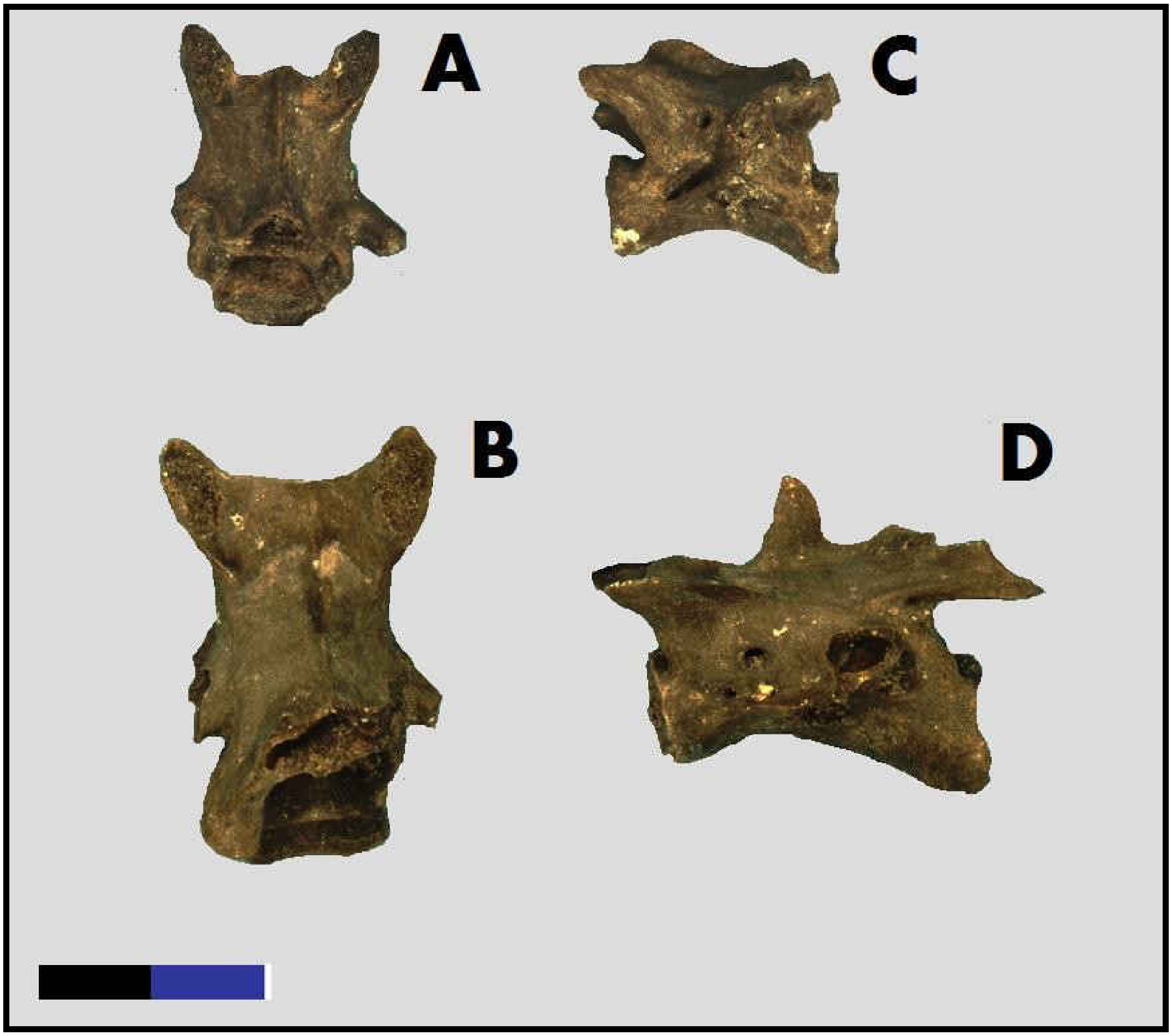

Figure 2.19. ETMNH 4922 *Plethodon*-type plethodontid Type A first trunk vertebra (T1) in A) dorsal and B) left lateral views; ETMNH 4932 *Plethodon*-type plethodontid Type B trunk vertebra in C) dorsal and D) left lateral views. Scale bar is 2 mm.

*Desmognathu*s sp.

Fossil material: 1 atlas (?) (ETMNH 1875); 15 mid-trunk vertebrae (ETMNH 1857, 1874, 1883-1886, 1889, 3844, 4930, 4931, 4937); 1 last trunk vertebra (?) (ETMNH 1890); 3 caudosacral vertebrae (ETMNH 1858, 1887, 1888). NIE = 20 and MNI = 2 (based on the number of caudosacrals).

Remarks:

Opisthocoelous vertebrae sharing general features with the modern *Desmognathus* and *Plethodon*-type plethodontid are here referred to *Desmognathus* sp.

ATLAS (AT). This fragmentary atlas is missing the entire neural arch and much of the atlantal cotyles, the odontoid process appears worn so it can not be said if it has articular facets. This specimen is tentatively referred to *Desmognathus* sp. based on the distinctly ventral location of the posterior cotyle relative to the odontoid process, though it is not as ventrally located as in modern *Desmognathus*. This atlas may represent a transitional form between the generalized plethodontid atlas and the unique atlas of modern *Desmognathus*.

MID-TRUNK VERTEBRAE (TM). These vertebrae are opisthocoelous and generally more robust than the *Plethodon*-type vertebrae described above. The posterior cotyles are larger than the anterior condyle and more ventrally placed. The neural canal and neural arch are similar to the *Plethodo*n-type, but the posterior portion of the neural arch is wider and higher with distinct neural ridges connecting to hypapophyseal ridges (see figure 2.20). The preszygapophyseal and postzygapophyseal articular facets are generally oval-shaped and more horizontally oriented. A number of the mid-trunk vertebrae have posterior hypophyses. The transverse processes are like

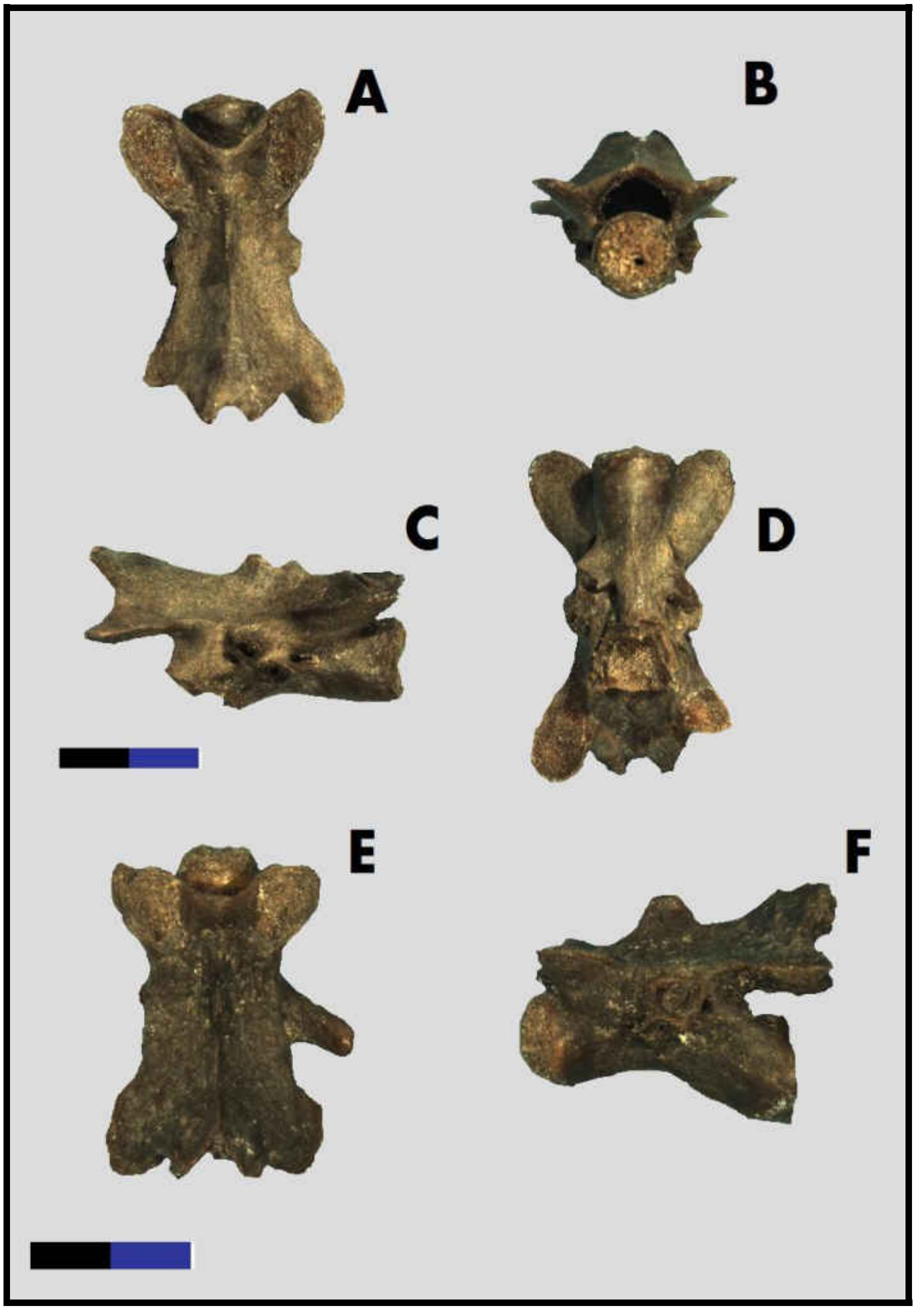

Figure 2.20. ETMNH 1874 *Desmognathus* sp. trunk vertebra in A) dorsal, B) anterior, C) right lateral, and D) ventral views; ETMNH 4930 *Desmognathus* sp. trunk vertebra in E) dorsal and F) left lateral views. Scale bars are 2 mm.

those in *Plethodon*-type. A single spinal nerve foramina is present posterior to the diapophyses.

POSTERIORMOST TRUNK AND CAUDOSACRAL VERTBRAE (TL and CS). These vertebrae are opisthocoelous but in general look like those found in *Plethodon*-type except with more ventrally placed posterior cotyles.

Subfamily Spelerpinae Cope, 1859

The plethodontid subfamily Spelerpinae (*sensu* Chippingdale et al. [2004]) is comprised of *Gyrinophilus*, *Stereochilus*, *Pseudotriton*, *Eurycea*, and *Haideotriton*.

Characters for the plethodontid subfamily Spelerpinae are given as exemplified by *Eurycea* (see Figure 2.21). Vertebrae generally have widely separated transverse processes (with parapophyses anterior to the diapophyses) that do not exceed the lateral extent of the zygapophyses (Miller, 1992; Holman, 2006). Vertebrae of many of the extant species examined appear opisthocoelous due to a calcified ring on the anterior cotyle, though in some specimens examined this ring had detached. The vertebrae of spelerpine plethodontids (except *Gyrinophilus*) have two spinal nerve foramina exiting posterior to the transverse processes in all trunk vertebrae except T1 (which has two spinal nerve foramina anterior to the transverse processes) and T2 (which has a spinal nerve foramina anterior to and two foramina posterior to the transverse processes).

Spelerpinae-type

Fossil material: 1 first trunk vertebra (ETMNH 1870); 1 third trunk vertebra (ETMNH 1869); 35 mid-trunk vertebrae (ETMNH 1867, 1868, 1891-1900, 7225-7236, 7238); 2 last trunk vertebrae

(ETMNH 1871, 7237). NIE = 39 and MNI = 2.

Remarks:

Amphicoelous trunk vertebrae exhibiting the above noted spinal nerve foramina patterns are here referred to Spelerpinae-type, otherwise differing from the *Plethodon*-type only in being more elongate with more symmetrical zygapophyseal articular facets and a lower neural arch profile (see Figure 2.22).

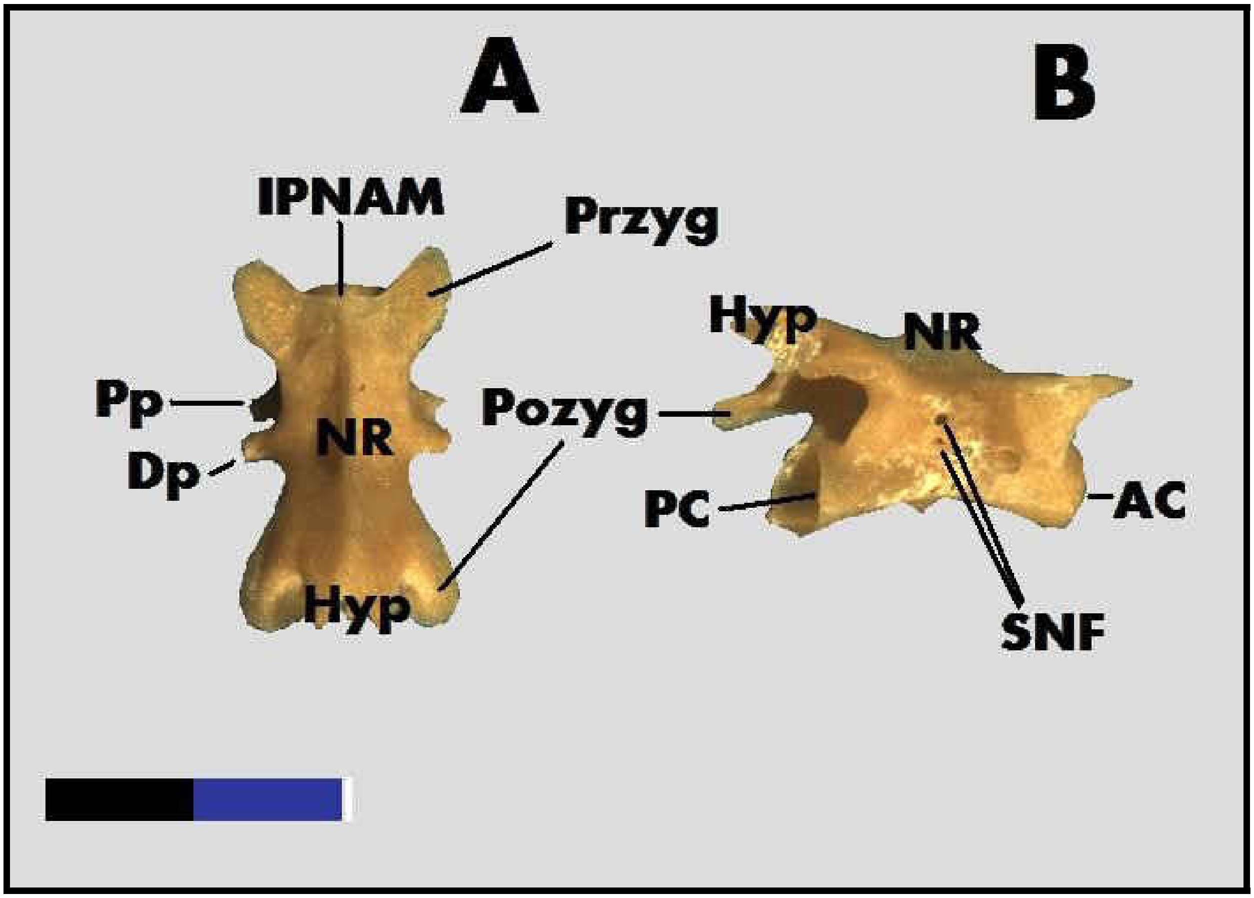

Figure 2.21. Generalized spelerpine plethodontid reference trunk vertebra (DCP 3694, *Eurycea guttolineata*) in dorsal and right lateral views illustrating features noted in descriptions: AC = anterior cotyle, Dp = diapophysis, Hyp = hyperapophyses, IPNAM = inter-prezygapophyseal neural arch margin, NR = neural ridge, PC = posterior cotyle, Pozyg = postzygapophyses, Pp = parapophysis, Przyg = prezygapophyses, SNF = spinal nerve foramina. Scale bar is 2 mm.

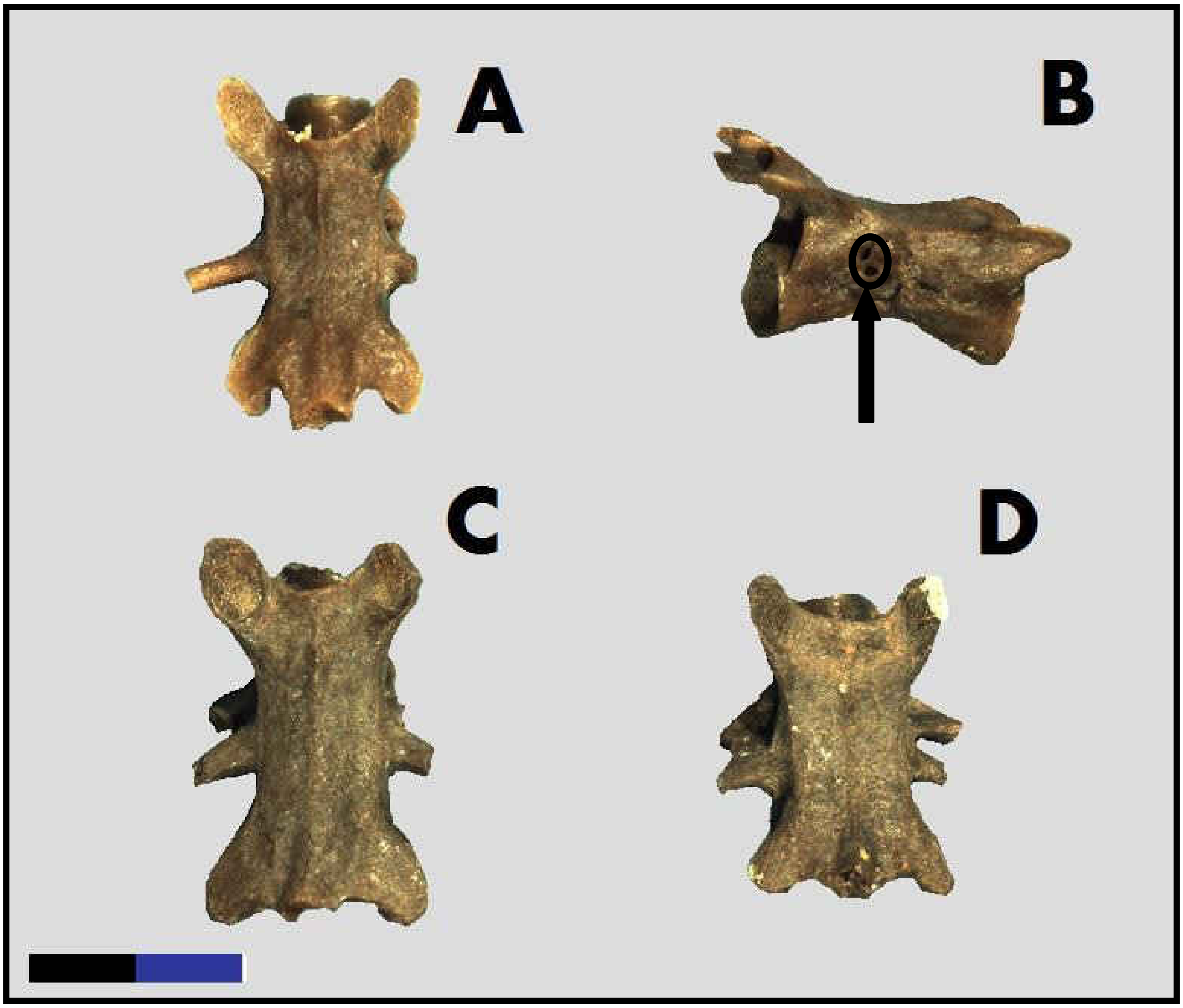

Figure 2.22. ETMNH 1868 Spelerpinae-type plethodontid trunk vertebra in A) dorsal and B) right lateral views, note double spinal nerve foramina (B); ETMNH 4934 Spelerpinae-type trunk vertebra in C) dorsal view; ETMNH 1871 Spelerpinae-like plethodontid last trunk vertebra (TL) in D) dorsal view. Scale bar is 2 mm.

Family Salamandridae Gray, 1825

Salamandrids (newts) are primarily found in Europe and Asia, with a few species in North America, Africa, and the Middle East (Wells, 2007). Most are semi-aquatic, breed in water, and usually live at least part of their lives on land (Wells, 2007). The North American *Notophthalmus* breed mostly in ponds, larvae transform into a terrestrial 'eft' stage, and then return to the pond several years later to breed as aquatic adults (Wells, 2007).

The vertebrae of salamandrids are fully opisthocoelous and have spinal nerve foramina exiting posterior to the transverse processes in all vertebrae except the first trunk vertebra (T1) which has spinal nerve foramina exiting both posterior to and anterior to the transverse processes (Edwards, 1976; Naylor, 1978).

Genus *Notophthalmus* Rafinesque, 1820

Eastern Newt

Reference specimen: 2 *Notophthalmus v. viridescens* (RWV 1803 and JIM 0824).

Vertebral Morphology:

The vertebrae of *Notophthalmus* have neural crests and hyperapophyses that are extremely tall and capped by flat, porous bone (see Figure 2.23). Though very similar in morphology to *Taricha* (the only other salamandrid genus in North America), *Notophthalmus* has linear to convex inter-prezygapophyseal neural arch margins. In *Taricha* this margin is concave, which makes distinguishing the two genera very simple. Of the three species of *Notophthalmus*, *N. viridescens* is unique in having a highly convex inter-prezygapophyseal neural arch margin (Miller, 1992), whereas the margin is linear in the others.

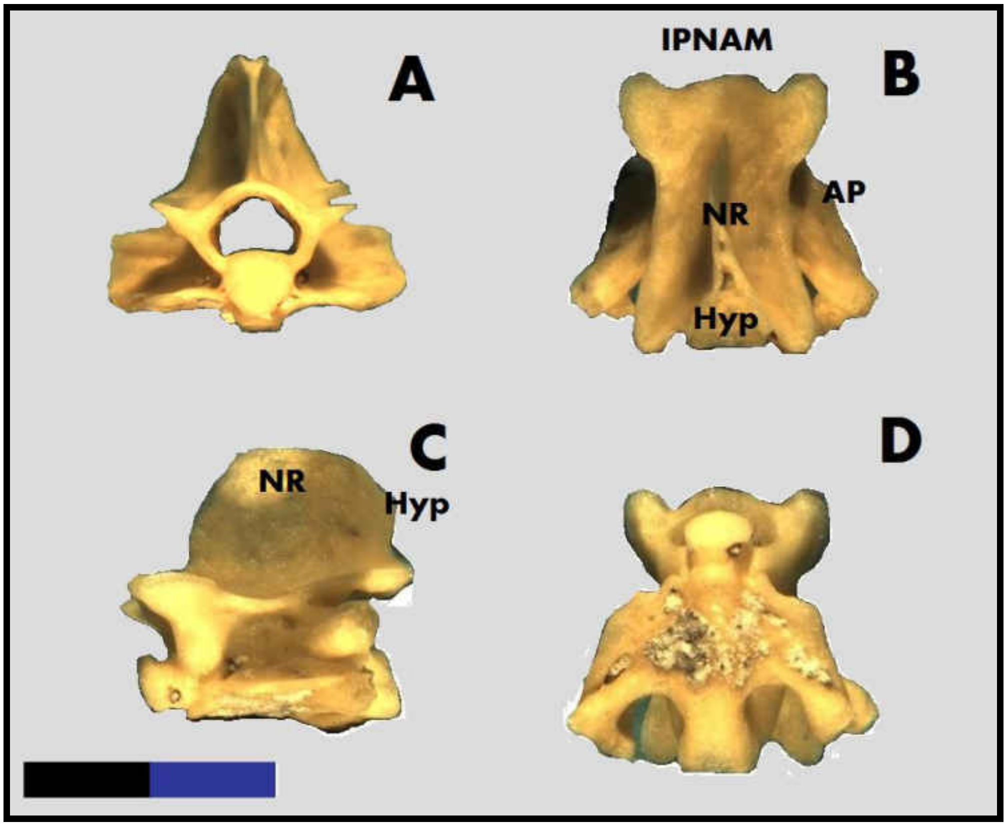

Figure 2.23. Reference (RWV 1803) *Notophthalmus viridescens viridescens* trunk vertebra in A) anterior, B) dorsal, C) left lateral, and D) ventral views. AP = alar process, Hyp = hyperapophysis, IPNAM = inter-prezygapophyseal neural arch margin, NR = neural ridge. Scale bar is 2 mm.

Notophthalmus sp.

Fossil material: 2 trunk vertebrae (ETMNH 3845 and 4919). NIE = 2 and MNI = 1.

Remarks:

These two opisthocoelous trunk vertebrae are referred to the genus *Notophthalmus*, rather than *Taricha*, primarily because they have convex inter-prezygapophyseal neural arch margins. The parapophyses of specimen ETMNH 4919 are connected to the centrum by well-developed ventral alar processes; these processes are less well-developed in ETMNH 3845 (Figure 2.24). The inter-prezygapophyseal neural arch margins of both specimens are distinctly convex, which according to Miller (1992) would seem to ally it with the living *N. viridescens*. If these specimens are *N. viridescens*, it would be the oldest account of the species. It should be noted, however, that *N. robustus*, a salamandrid reported by Estes (1963) from the Early Miocene of Florida, also has a convex inter-prezygapophyseal neural arch margin and is of similar proportions. The likelihood that the GFS salamandrid is *N. viridescens* or *N. robustus* seems equally as likely, consequently the specimens are referred to *Notophthalmus* sp. Regardless, this is the earliest fossil account of the family and genus in Tennessee, and the only Mio-Pliocene record for the genus *Notophthalmus*.

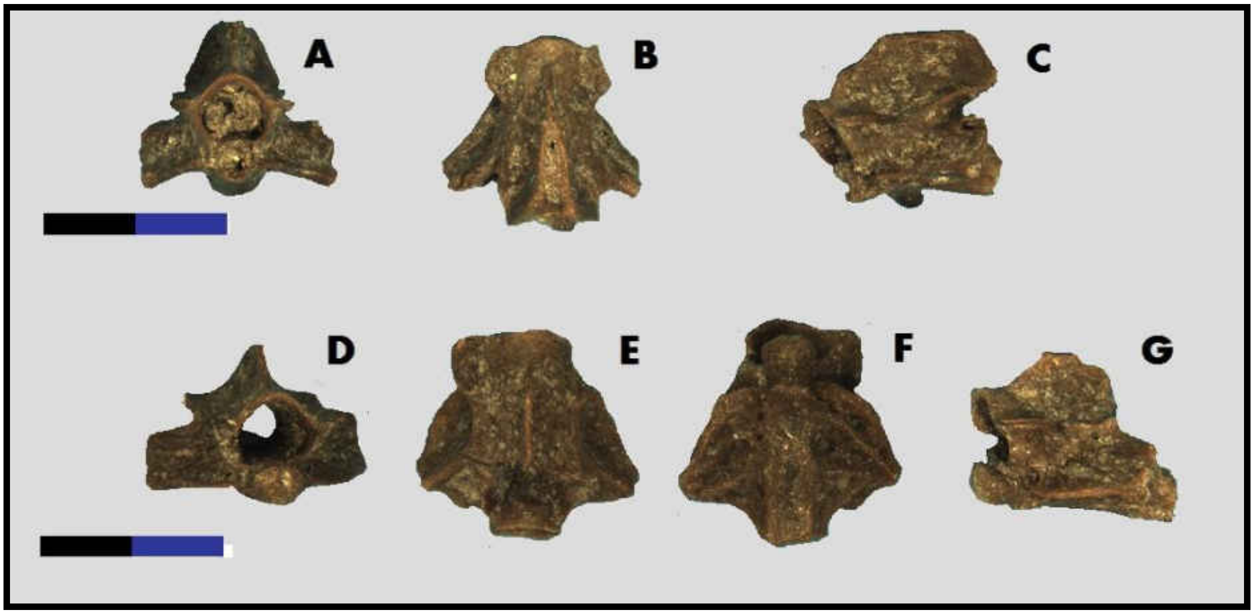

Figure 2.24. ETMNH 3845 *Notophthalmus* sp. trunk vertebra in A) anterior, B) dorsal, and C) left lateral views; ETMNH 4919 *Notophthalmus* sp. trunk vertebra in D) anterior, E) dorsal, F) ventral, and G) left lateral views. Scale bars are 2 mm.

Discussion

The salamander fauna recovered from the Gray Fossil Site represents the most taxon-rich salamander fauna in Pre-Pleistocene North America, and is the earliest record of salamander fossils from the Appalachian Mountain region. The fauna contains at least five distinct taxa, and represents the earliest record of Ambystomatidae and Plethodontidae east of the Mississippi River and the second earliest record of the salamandrid genus *Notophthalmus* (the earliest east of the Mississippi being the Hemingfordian *N. robustus* of Florida).

The difficulty with identifying fossil plethodontids below the family level is not resolved by this study; however, the use of observed subfamily characters allows for reference to 'type'. Attribution to species for *Ambystoma* and *Notophthalmus* is avoided in this report to reflect a departure from the tendency to identify fossil taxa based on locally endemic modern species.

Paleoecology

In holding with Schubert and Wallace (2006), paleoecological inferences are based primarily on phylogenetic bracketing (i.e. inferring habitat preference based on family membership) when taxa cannot be identified to genus (as is the case with the GFS plethodontids), and by more direct analogy in cases where genus can be determined (i.e. *Ambystoma* sp. and *Notophthalmus* sp.). Extant *Notophthalmus viridescens* inhabit coniferous and deciduous forests, with immature larvae and adult newts living in small bodies of freshwater and the juvenile “eft” stage inhabiting the shorelines and woodland habitats around these bodies of water (Petranka, 1998). GFS *Notophthalmus* sp., assuming analogous habitat preference, supports the wooded-pond environment interpretation of DeSantis and Wallace (2006, 2008). Extant *Ambystoma* species can be found in upland mixed and coniferous forests that are sufficiently damp and have bodies of water suitable for breeding, and places where they are able to burrow in the soil or find burrows made by other animals (Petranka, 1998). Thus, the presence of *Ambystoma* sp. garners more support for the wooded-pond interpretation of the GFS. Plethodontid salamanders (plethodontine and spelerpine alike) in general prefer wooded moist habitats, whether or not they have aquatic larvae (Petranka, 1998; Wells, 2007). Unfortunately, this paleoenviornmental interpretation based on the salamander fauna is no more resolved than that of Schubert and Wallace's (2006) analysis utilizing the entire herpetofauna. This lack of resolution is due to our inability to identify salamander taxa below genus level at the GFS.

The faunal composition as represented by the preliminary sample is predominated by presumably terrestrial, direct-developing plethodontids (see Figure 2.25) and underscored by ambystomatids (some of which are considered neotenic) and desmognathine plethodontids (which may or may not be semi-aquatic to aquatic in habit). The genus *Desmognathus* was proposed by Tihen and Wake (1981) and supported by Chippindale et al. (2004) to have split from the rest of the Plethodontinae 7 million years ago; the *Desmognathus* sp. at the GFS would seem to support this date by its presence. The *Ambystoma* sp., *Desmognathus* sp., and some of the Type B *Plethodon*-type plethodontids fall into a similarly large size range (estimated around 20 cm in total length by comparison with modern specimens), presenting the potential for niche partitioning and a base for ecological interpretation revolving around competition of similar sized taxa. In terrestrial environments dominated by similar sized plethodontids and ambystomatids, it has been proposed that competition pushes some taxa to utilize an unexplored niche (in this case the aquatic niche): which would explain the neotenic individuals of *Ambystoma* sp. and potentially the *Desmognathus* sp. as well (if one follows the 'body size gradient' noted by Wells

(2007) in which larger bodied desmognathines are more aquatic in habit). This style of partioning might also support the idea that terrestrial competition was the impetus for the origin of the genus *Desmognathus* and reacquisition of aquatic larvae in more derived desmognathines (Lombard and Wake, 1986; Chippindale and Wiens, 2005; Vieites et al., 2007).

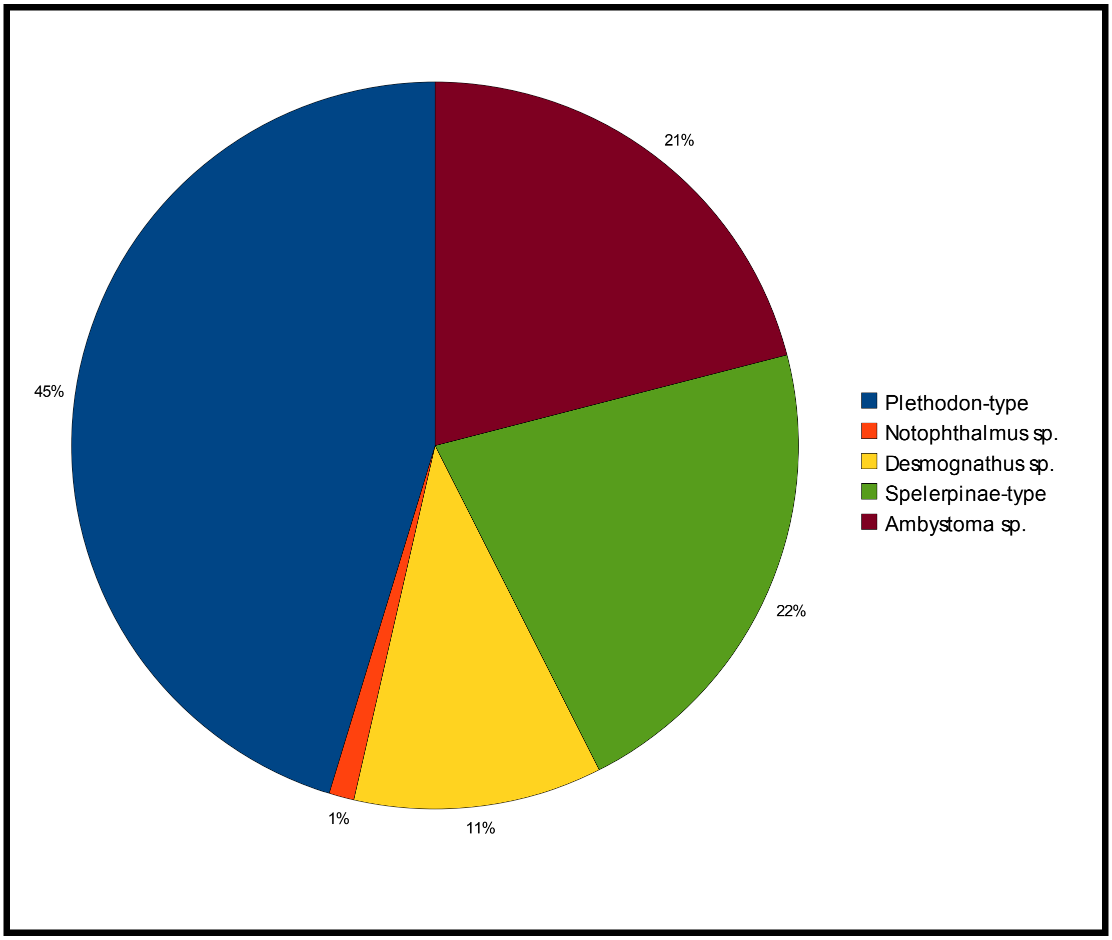

Figure 2.25. Pie chart showing the relative abundances of salamander pre-caudal vertebrae by taxa from the GFS sample. Plethodontids account for 78% of the analyzed sample.

Paleobiogeography and Evolutionary History

The Pleistocene and Holocene fossil record for ambystomatids, plethodontids, and salamandrids is well represented in the southern Appalachians and much has been reported on changes in biogeography during this time frame (see references in Holman, 2006). Therefore, the presence of these families in the Mio-Pliocene of the southern Appalachians is not surprising. While these new records represent the earliest occurences of these taxa in the region, they provide limited information from a paleobiogeographical or evolutionary history standpoint. In essence, the only taxon present at the GFS that warrants special attention is the *Desmognathus* sp., being the oldest specimens referable to the genus *Desmognathus*. In terms of evolution, this taxon type stands out as potential support for an Appalachian origin for the group; though the possibility that this group could have its origin outside of the region cannot be discounted given the scant nature of plethodontid remains from this period (or any period prior to the Pleistocene for that matter).

Summary

The major findings of this study of the salamander fauna at the Mio-Pliocene Gray Fossil Site are as follows:

1) At least five fossil salamander taxa are identified at the GFS: *Ambystoma* sp., *Notophthalmus* sp., *Plethodon*-type plethodontid (with possibly two forms), *Desmognathus* sp., and Spelerpinae-type plethodontid; making the GFS the most diverse pre-Pleistocene salamander fauna in North America.
2) GFS specimens represent the earliest fossil record of salamanders in the Appalachian Mountain region.

3) *Notophthalmus* sp. is the second oldest record of the genus east of the Mississippi River, and the only Mio-Pliocene record of the genus.
4) The GFS plethodontids represent the earliest record of the family east of the Mississippi River (being that GFS is older than the Pipe Creek Sinkhole of Indiana).
5) GFS *Desmognathus* sp. represents the earliest fossil record of the genus *Desmognathus*.
6) The faunal assemblage supports earlier interpretations of the GFS as a wooded-pond environment.

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CHAPTER 3

CONCLUSIONS

Summary

The major findings of this study of the salamander fauna at the Mio-Pliocene Gray Fossil Site are summarized as follows:

1) At least five fossil salamander taxa are identified at the GFS: *Ambystoma* sp., *Notophthalmus* sp., *Plethodon*-type plethodontid (with possibly two forms), *Desmognathus* sp., and Spelerpinae-type plethodontid; making the GFS the most diverse pre-Pleistocene salamander fauna in North America.
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4) The GFS plethodontids represent the earliest record of the family east of the Mississippi River (being that GFS is older than the Pipe Creek Sinkhole of Indiana).
5) GFS *Desmognathus* sp. represents the earliest fossil record of the genus *Desmognathus*.
6) The faunal assemblage supports earlier interpretations of the GFS as a wooded-pond environment.

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APPENDIXES

Appendix A: Glossary of Terminology

Alar process: a flat or wing-like process, usually extending from the ventral portion of the parapophysis to the centrum.

Amphicoelous: condition in which the vertebral centrum is hollow at each end.

Articular facet: a depression in the bone permitting articulation with another bone.

Atlantal: referring to the atlas.

Atlantal cotyles: the paired anterior facets on the atlas which articulate with the occipital condyles of the skull.

Atlas: the single cervical (neck) vertebra.

Basapophyses: paired ventro-lateral processes positioned on the anterior or posterior portion of the centrum.

Caudal vertebra: a tail vertebra.

Caudosacral vertebra: one of several vertebrae occurring posterior to the sacrum and anterior to the first caudal vertebra.

Centrum: body of the vertebra below the neural canal.

Diapophysis: upper member of paired rib articulations found on each side of a vertebra.

Hyperapophysis (neural spine of some authors): posterior projection(s) of the neural arch between the postzygapophyses.

Hypophysis: a median ventral process of the centrum which can be spine-like or ridge-like.

Mid-trunk vertebrae: any vertebra occurring between the third vertebra and the last trunk vertebra.

Neural arch: the structure arising from the top of the centrum surrounding the neural canal.

Neural canal: the canal for the spinal cord, that passes under the neural arch and above the centrum of each vertebra.

Neural ridge (neural crest): a dorsal, ridge-like process arising at the midline of the neural arch.

Neoteny: retention of larval features (such as external gills) into sexual maturity.

Notochord: fibrous support structure in larval vertebrates prior to development of the bony vertebral column.

Notochordal canal: canal for the notochord which passes through the middle of the vertebral centrum, this canal is interrupted and closes off as vertebrates mature.

Opisthocoelous: condition in which the anterior portion of the vertebral centrum is filled with compact bone while the posterior portion is hollow.

Odontoid process: a cup- or knob-shaped anterior projection of the atlas that articulates with the ventro-medial surface of the foramen magnum of the skull.

Parapophysis: the lower member of paired rib articulations found on each side of a vertebra.

Postzygapophyses: pair of posterior processes bearing ventral articular facets that articulate with the prezygapophyses of the following vertebra.

Prezygapophyses: pair of anterior processes bearing dorsal articular facets that articulate with the postzygapophyses of the preceding vertebra.

Sacrum: vertebra which supports the pelvic girdle.

Spinal nerve foramen: an opening in the neural arch through which a spinal nerve exits the neural canal.

Trunk vertebra: any vertebra occurring after the posterior to the atlas and anterior to the sacrum.

Transverse processes: the diapophyses and parapophyses, these structures articulate with rib heads.

Appendix B: Institutional and Collection Abbreviations

ETMNH: East Tennessee Museum of Natural History

RWV: collection of R. Wayne Van Devender

BWS: collection of Blaine W. Schubert

JIM: collection of Jim I. Mead

ASU: Appalachian State University

CMNH: Carnegie Museum of Natural History

UCMVZ: University of California Museum of Vertebrate Zoology

TRVD: collection of T.R. Van Devender

FB: Field Book number

DCP: collection of Dennis C. Parmley

NJSM: New Jersey State Museum

VITA

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