



First Mio-Pliocene salamander fossil assemblage from the southern Appalachians

Grant S. Boardman and Blaine W. Schubert

ABSTRACT

The Gray Fossil Site (GFS) of northeastern Tennessee has yielded a diverse salamander fossil assemblage for the southern Appalachian Mio-Pliocene. This assemblage includes at least five taxa (*Ambystoma* sp.; *Plethodon* sp., Spelerpinae, gen. et sp. indet., *Desmognathus* sp.; and *Notophthalmus* sp.) from three families (Ambystomatidae, Plethodontidae, and Salamandridae, respectively). All taxa are present in the area today and support a woodland-pond interpretation of the site. Reported 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.

Grant S. Boardman. Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska, 68588, USA and Don Sundquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, Tennessee, 37614, USA grant128@hotmail.com

Blaine W. Schubert. Department of Geosciences and Don Sundquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, Tennessee, 37614, USA schubert@mail.etsu.edu

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INTRODUCTION

Three salamander families are reported from the Mio-Pliocene Gray Fossil Site (GFS), Washington County, Tennessee (Figure 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 Mio-Pliocene records of the family

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FIGURE 1. Location of the Gray Fossil Site, Tennessee, USA. From DeSantis and Wallace (2008).

have been reported east of the Rockies, a single '*Plethodon*-like' trunk vertebra from Coffee Ranch, Texas (Parmley 1989) and indeterminate 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 of North America, but is 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 assemblage in an upland environment. The fossil site covers roughly 1.8-2.0 ha, and fossiliferous sediments are as thick as 39 m (Wallace and Wang 2004; Nave et al. 2005). The site is composed 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). The date of the GFS is inferred to be about 4.5 – 7 m.y.a. based on the co-occurrence of the rhinoceros *Teleoceras* and the tremarctine bear *Plionarctos* (Wallace and Wang 2004). The bulk of the herpetofauna (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), Jiang and Liu (2008), and Liu and Jacques (2010), 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 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 eastern North America. This paper represents a revised version of Boardman (2009).

MATERIALS AND METHODS

Fossil Collection and Identification

Vertebrate microfossil remains were collected by water screening matrix from 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. Though salamander cranial and postcranial materials are known from the GFS, they are exceedingly rare and difficult to identify below family level; so vertebrae are used exclusively for identification purposes in this study.

Identification of fossil salamander skeletal elements is complicated by the overall simplicity of salamander bones in general, phylogenetic/ontogenetic variation, and similarity between unrelated taxa. The inferred age of the GFS (about 4.5 – 7 m.y.a.), and lack of specific morphological characters, makes species attribution based on vertebrae seemingly implausible. For these reasons fossil taxa are identified to the level of genus where possible. Because vertebrae are the most numerous elements in the skeleton and the most represented fossil element for this group 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 verte-

brae), and caudal region (with a variable number of vertebrae from 20 to more than 100). GFS salamander vertebrae were identified by comparing the fossil material with modern specimens from all families and literature on various modern and fossil 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 East Tennessee State University Vertebrate Paleontology Laboratory (ETVP).

After preliminary examination of both modern comparative and fossil specimens, and literature regarding vertebral characters of extinct families (e.g., the Batrachosauroididae), it was clear that none of the analyzed fossil specimens represented extinct families. Following this finding, two assumptions are posited in regards to identity of GFS specimens: 1) specimens represent extant families (i.e., no Batrachosauroididae), and 2) the presence of spinal nerve foramina posterior to the transverse processes in examined fossil trunk vertebrae limited identifications to members of the extant families Ambystomatidae, Plethodontidae, Salamandridae, and Sirenidae (as noted by Edwards 1976). Where identifications are made to gen. et sp. indet., further identification is discussed but left for future work due to a lack of confidence in generic level characters.

Data Analysis

Screening and sorting of fossil rich sediment at the GFS is an ongoing process so salamander vertebrae are continually recovered. Thus, the analysis here is based on a sample from the fossil site. Though this sample may not be entirely reflective of taxon abundance or diversity, it does give a preliminary view of the GFS salamander assemblage. Relative abundances of fossil salamander taxa are represented in two ways, 1) the number of identified elements for the taxon (NIE), and 2) minimum number of individuals for the taxon (MNI). 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.

Systematic Accounts

A total of 181 pre-caudal vertebrae were identified and 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 recovered 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 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).

SYSTEMATIC PALEONTOLOGY

Order CAUDATA Oppel, 1810

Suborder SALAMANDROIDEA Noble, 1931

Family AMBYSTOMATIDAE Hallowell, 1856

Genus *AMBYSTOMA* Tschudi, 1838

The family Ambystomatidae is comprised of one genus, *Ambystoma*, and approximately 32 species (AmphibiaWeb 2011). 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 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). Neotenic populations also occur in temperate, low altitude regions with permanent bodies of water lacking large-bodied predatory fish (Petranka 1998; Lannoo 2005; Wells 2007).

Vertebral Morphology

Vertebrae of *Ambystoma* are amphicoelous 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. 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. 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. 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, except that the transverse processes are directed dorsally rather than ventrally (Miller 1992). For both the TL and CS the transverse processes are acuminate. 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 (Olori and Bell 2007).

Ambystoma sp.
Figures 2 – 7

Referred specimens. 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 large transverse processes, V-shaped inter-prezygapophyseal neural arch margins, and notably elevated posterior portion of the neural arch are 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*, 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; 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.

First trunk vertebra (T1). Posterior and anterior cotyles are circular. Neural canal is large and constricted dorsally, the canal openings are nearly triangular. The anterior half of the neural arch is horizontal (i.e., flat) with a slightly raised neural crest, whereas the posterior half is rising about 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 originates in the middle of the centrum and the diapophyses in the middle of the neural arch wall. The diapophyses are ventrally constricted. There is a single spinal nerve foramina posterior to the diapophyses; vascular foramina are present.

Mid-Trunk vertebrae (TM). These vertebrae have anterior and posterior cotyles that are circular and many have basapophyses. The neural canal is roughly circular and becomes more flattened in the posterior vertebrae. The anterior half of the neural arches is 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. Like the T2 and T3 vertebrae, 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, a feature expressed by neotenic individuals (Tihen 1942; Holman 1975; Holman 2006).

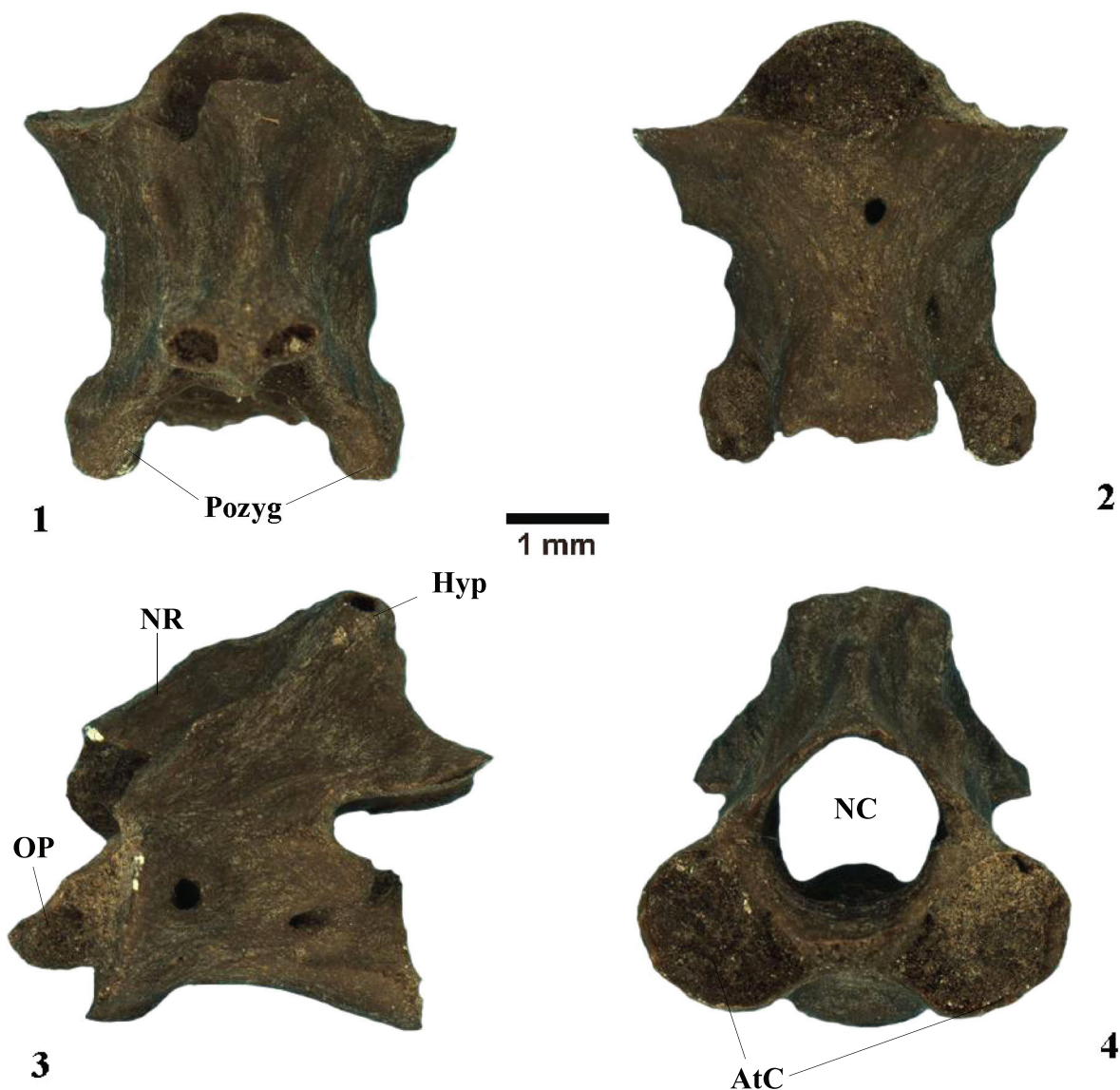


FIGURE 2. ETMNH 3852, *Ambystoma* sp. atlas in (1) dorsal, (2) ventral, (3) left lateral, and (4) anterior views. Osteological abbreviations: AtC, atlantal cotyle; Hyp, hyperapophysis; NC, neural canal; NR, neural ridge; OP, odontoid process; Pozyg, postzygapophysis.

Posteriormost trunk vertebrae (TL). This vertebra is 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 rises less than 45 degrees to meet the hyperapophysis. 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 trans-

verse 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 vertebrae are 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

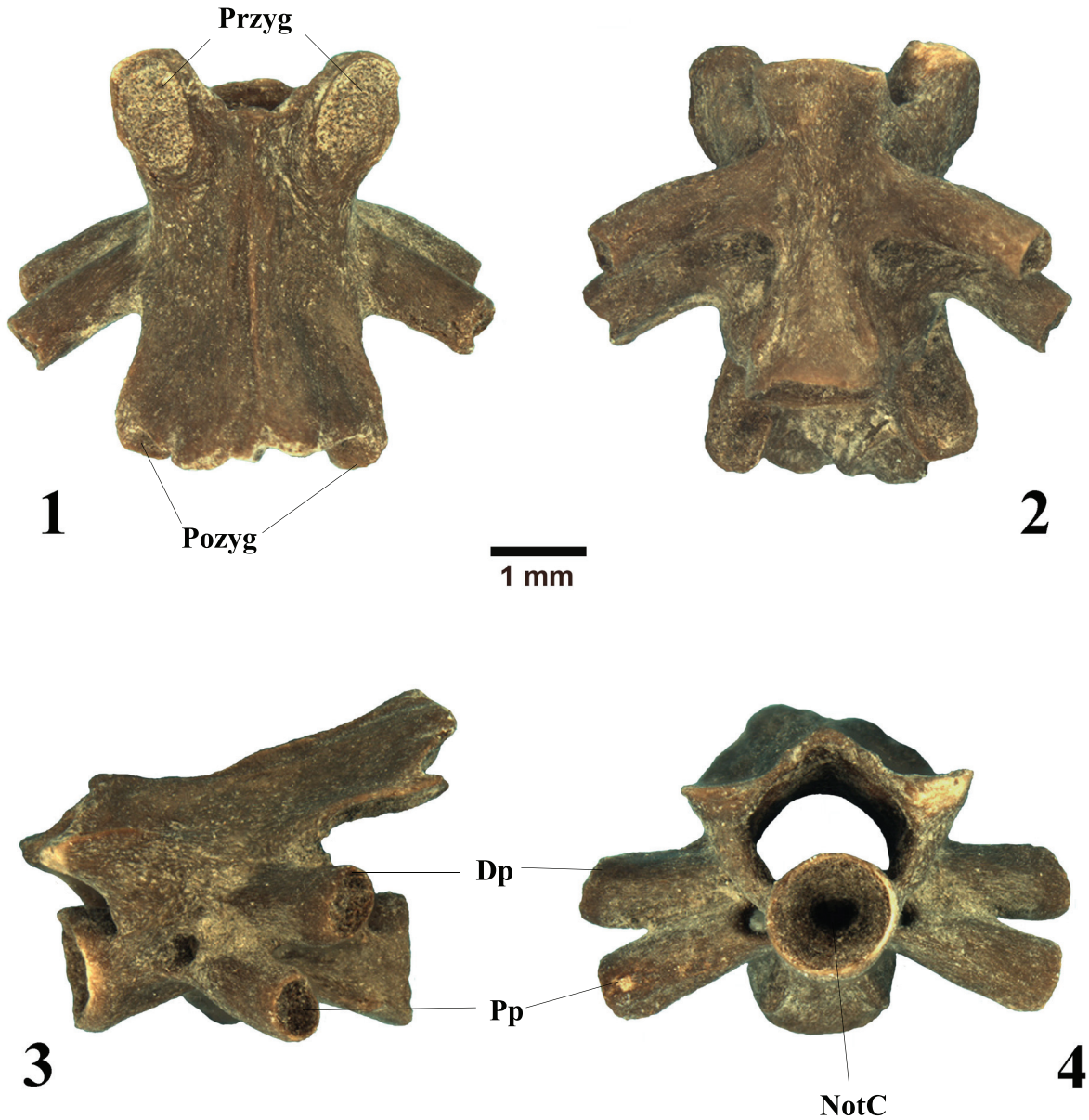


FIGURE 3. ETMNH 3857, *Ambystoma* sp. first trunk vertebra in (1) dorsal, (2) ventral, (3) left lateral, and (4) anterior views. Osteological abbreviations: Dp, diapophysis, NotC, notochordal canal; Pozyg, postzygapophysis; Pp, parapophysis; Przyg, prezygapophysis.

the neural arch rises less than 45 degrees to meet the hyperapophysis, that extends beyond the posterior margin of the postzygapophyses. The interprezygapophyseal 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 foramina posterior to the diapophyses. Several sacral vertebrae may be representative of small- to medium-sized neotenic individuals of *Ambystoma* sp., 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



FIGURE 4. ETMNH 4917, *Ambystoma* sp. trunk vertebra exhibiting an open notochordal canal indicative of neoteny in (1) dorsal, (2) anterior, (3) posterior, and (4) left lateral views.

neotenic plethodontids can be examined, these specimens will remain tentatively in *Ambystoma* sp.

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

Family PLETHODONTIDAE Gray, 1850

The salamander family Plethodontidae is the 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).

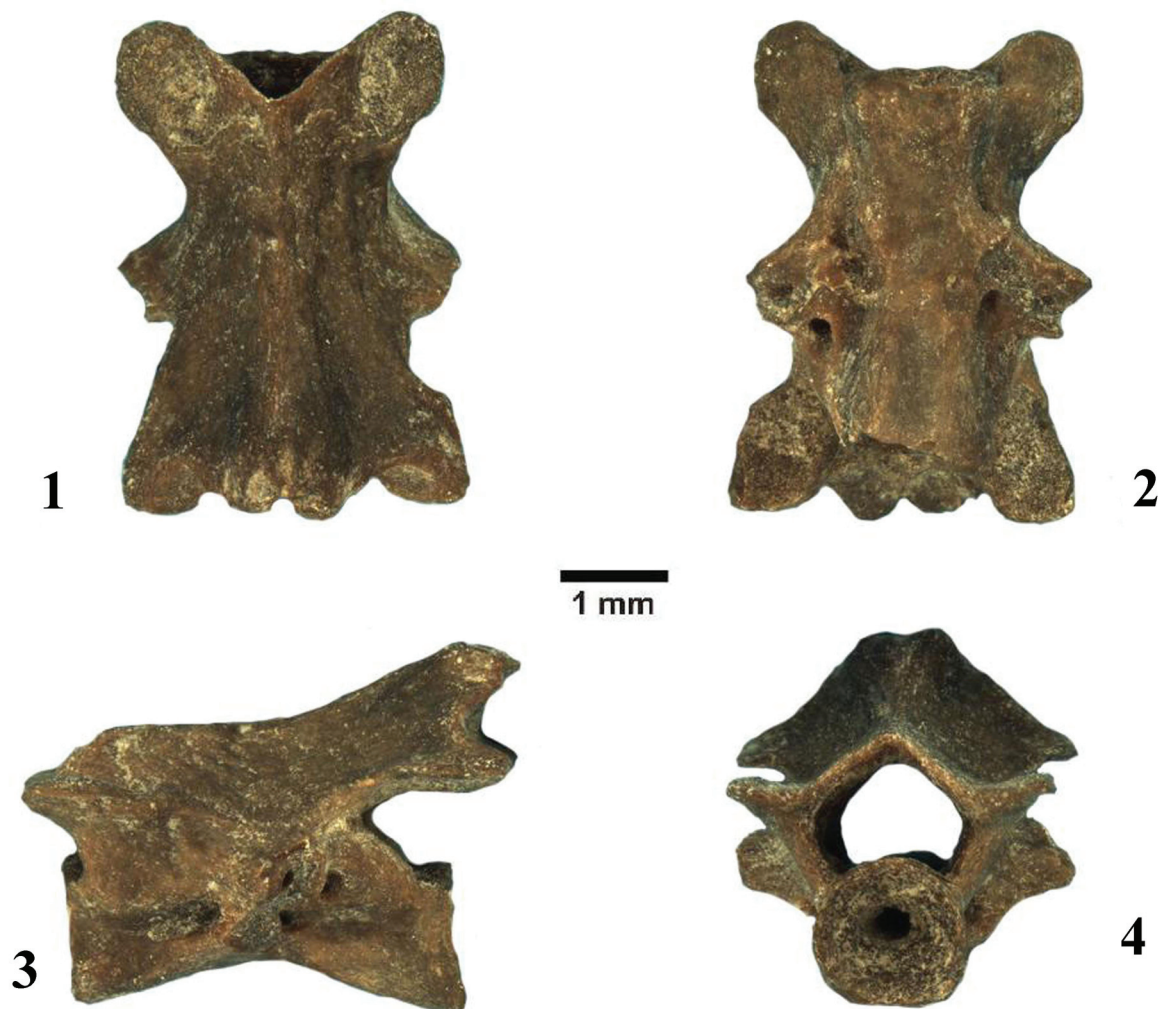


FIGURE 5. ETMNH 3858, *Ambystoma* sp. anterior trunk vertebra in (1) dorsal, (2) ventral, (3) left lateral, and (4) anterior views.

Vertebral Morphology

Plethodontid atlantes have odontoid processes with paired articular facets, 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). The 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 (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. 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). 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, a character used by Olori and Bell (2007) to distinguish plethodontids from some of the more gracile ambystomatids.



FIGURE 6. ETMNH 3856, *Ambystoma* sp. last trunk vertebra in (1) ventral, (2) dorsal, (3) left lateral, and (4) posterior views.

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 sp.
Figures 8 – 9

Referred specimens. 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 verte-

brae (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, and agreeing in character with *Plethodon* and *Ensatina* rather than non-plethodontine plethodontids, are here referred to



FIGURE 7. ETMNH 3855, *Ambystoma* sp. sacral vertebra in (1) dorsal, (2) ventral, (3) anterior, and (4) right lateral views.

Plethodon sp. Two morphotypes are noted for this taxon, though there is clearly both size and morphological cause for considering them separate taxa, we retain this identification until further detailed comparisons are made with modern *Plethodon* species.

Atlas (AT). The *Plethodon* sp. atlantes come in two forms: Type A and Type B. Both atlantal morphotypes have odontoid processes with paired articular facets (which clearly distinguish both from the atlantes of ambystomatids). Type A (the smaller form) has circular atlantal cotyles which are laterally placed, and Type B (the larger 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. None of the atlantal specimens have well-preserved postzygapophy-

ses, so little can be said about their general shape or orientation.

First trunk vertebra (T1). 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. 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.



FIGURE 8. ETMNH 3847, *Plethodon* sp. Type A atlas in (1) right lateral and (2) ventral views, and ETMNH 4920, *Plethodon* sp. Type B atlas in (3) right lateral and (4) ventral views.

Second trunk vertebra (T2). These trunk vertebrae 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 appears to share the features of the first two trunk vertebrae except that it has a single spinal nerve foramina posterior to the diapophyses.

Mid-Trunk vertebrae (TM). These vertebrae are 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. 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 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.



FIGURE 9. ETMNH 4922, *Plethodon* sp. Type A first trunk vertebra in (1) dorsal and (2) right lateral views and ETMNH 4932, *Plethodon* sp. Type B trunk vertebra in (3) dorsal and (4) right lateral views.

Posteriormost trunk vertebrae (TL). These vertebrae 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 trunk vertebrae except that their transverse processes are completely fused, acuminate, and connected to the centrum by ventral alar processes.

Genus *DESMOGNATHUS* Baird, 1850
Desmognathus sp.
 Figure 10

Referred specimens. 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 modern *Desmognathus* 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 cannot 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*, it is more ventrally located than in other modern plethodontids (and other salamanders). This atlas may represent a transitional form between the gen-



FIGURE 10. ETMNH 1874, *Desmognathus* sp. trunk vertebra in (1) dorsal and (2) right lateral views, and ETMNH 4930, *Desmognathus* sp. trunk vertebra in (3) dorsal and (4) right lateral views.

eralized plethodontid atlas and the atlas of modern *Desmognathus*.

Mid-Trunk vertebrae (TM). These vertebrae are generally more robust than the *Plethodon* sp. vertebrae described above. The posterior cotyles are larger than the anterior condyle and more ventrally placed than those of *Plethodon* sp. and other plethodontids, a morphological arrangement diagnostic to *Desmognathus* (Holman, 2006). The neural canal and neural arch are similar to the *Plethodon* sp., but the posterior portion of the neural arch is wider and higher with distinct neural ridges connecting to hypapophyseal ridges, a feature also diagnostic to *Desmognathus* (Holman 2006). The preszygapophyseal and postzygapophyseal articular facets are generally oval-shaped and more horizontally oriented. A number of the mid-trunk vertebrae have posterior hypophyses, another feature diagnostic to *Desmognathus*. The transverse processes are like those in *Plethodon* sp. A single spinal nerve foramina is present posterior to the diapophyses.

Posteriormost trunk and caudosacral vertebrae (TL and CS). These opisthocoelous vertebrae match the overall morphology of *Desmognathus*.

Subfamily SPELERPINAЕ 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*. 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. Conforming with the observations of Edwards (1976), the vertebrae of spelerpine plethodontids (except *Gyrinophilus*) diagnostically have two spinal nerve foramina exiting posterior to the transverse processes in all

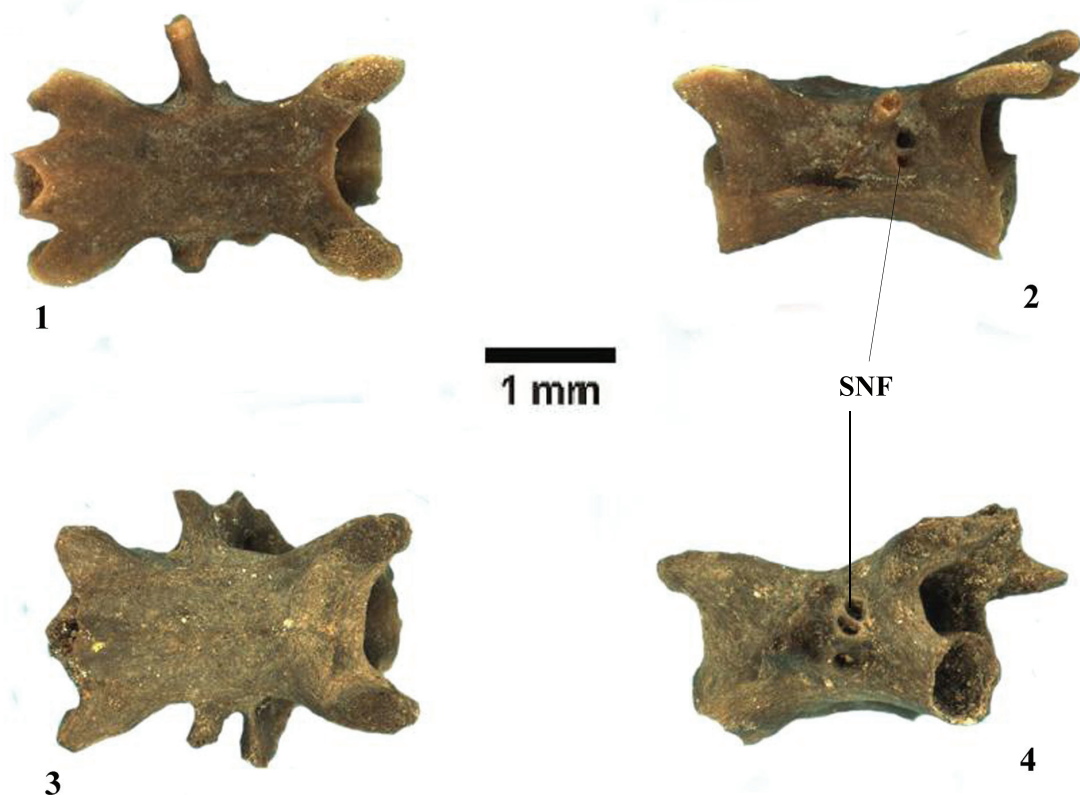


FIGURE 11. ETMNH 1868, Spelerpinae, gen. et sp. indet. vertebra in (1) dorsal and (2) left lateral views, and ETMNH 1871, Spelerpinae, gen. et sp. indet. last trunk vertebra in (3) dorsal and (4) left lateral views. Osteological abbreviation: SNF, spinal nerve foramen.

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, gen. et sp. indet.
Figure 11

Referred specimens. 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 diagnostic double spinal nerve foramina pattern of the subfamily Spelerpinae are here referred to Spelerpinae, gen. et sp. indet., otherwise differing from the *Plethodon* sp. only in being more elongate

with more symmetrical zygapophyseal articular facets and a lower neural arch profile.

Family SALAMANDRIDAE Gray, 1825

Salamandrids (true salamanders and 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 and reside 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).

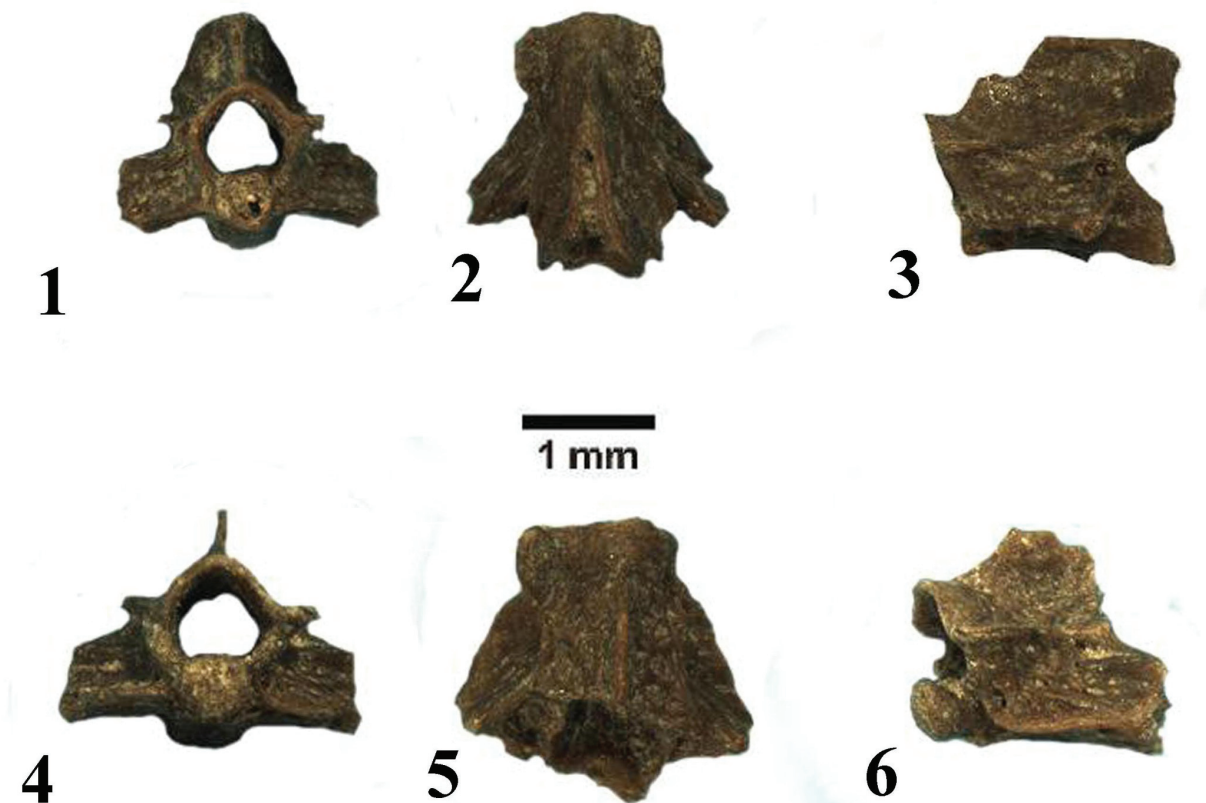


FIGURE 12. ETMNH 3845, *Notophthalmus* sp. trunk vertebra in (1) anterior, (2) dorsal, and (3) left lateral views, ETMNH 4919, *Notophthalmus* sp. trunk vertebra in (4) anterior, (5) dorsal, and (6) left lateral views.

Genus *NOTOPHTHALMUS* Rafinesque, 1820

The vertebrae of *Notophthalmus* have neural crests and hyperapophyses that are extremely tall and capped by flat, porous bone. 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.

Notophthalmus sp.
Figure 12

Referred specimens. 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. The inter-prezygapophyseal neural arch margins of both specimens are distinctly convex which, according to Miller (1992), would ally the GFS specimens 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 greater Appalachian region, and the only Mio-Pliocene record for the genus *Notophthalmus*.

DISCUSSION

The salamander assemblage recovered from the GFS represents the earliest Cenozoic record of salamander fossils from the Appalachians (a region well-known for its current salamander diversity). The fauna contains at least five distinct taxa, and represents the earliest record of Ambystomidae and Plethodontidae east of the Mississippi River, and the earliest record of the salamandrid genus *Notophthalmus* east of the Mississippi River and north 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

Our paleoecological interpretation based on the salamanders assumes that the described taxa co-occurred. At this point we feel this assumption is justified because all excavations have been in the same type of lake deposit, and represented vertebrate and plant species are consistent from one pit to another.

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, particularly along streamsides, whether or not they have aquatic larvae (Petranka 1998; Wells 2007). This paleoenvironmental interpretation based on the salamanders 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 the recovered salamander vertebrae below genus level.

The faunal composition as represented by the preliminary sample is predominated by terrestrial plethodontids and underscored by ambystomatids (with a mixed population of both neotenic and metamorphosed adults) and desmognathine plethodontids (which may or may not be semi-aquatic to aquatic in habit). The *Ambystoma* sp., *Desmognathus* sp., and some *Plethodon* sp. fall into a similarly large size range (estimated around 20 cm in total length by comparison with modern specimens), presenting the potential for adult niche partitioning and a base for ecological interpretation revolving around partitioning of similar sized taxa. This may 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 (see Lombard and Wake 1986; Chippindale and Wiens 2005; Vieites et al. 2007). Neoteny in part of the *Ambystoma* sp. population is likely attributable to lack of large-bodied predatory fish (Woodward, personal commun., 2010) and pond permanence. Pond permanence is evidenced by the non-existence of mud cracks in the strata and supported by the abundance of large bodied *Rana* that are indistinguishable from *R. catesbeiana* (bullfrog). Today bullfrogs require permanent bodies of water to survive their larval stage, which may last as long as 3 years, and always requires overwintering (Bruening 2002; Wells 2007).

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 biogeography during this time frame (see references in Holman 2006). Therefore, the presence of these families and genera in the Mio-Pliocene of

the southern Appalachians is not surprising. While these new records represent the earliest occurrences 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 biogeographic/evolutionary attention is the *Desmognathus* sp., being the oldest specimens referable to the genus *Desmognathus*. 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 may support this date by its presence. In terms of evolution, this taxon 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).

CONCLUSIONS

1. At least five fossil salamander taxa are identified at the GFS: *Ambystoma* sp., *Notophthalmus* sp., *Plethodon* sp. (with at least two morphotypes), *Desmognathus* sp., and Spelerpinae, gen. et sp. indet.; 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.
5. GFS *Desmognathus* sp. represents the earliest fossil record of the genus *Desmognathus*.
6. The salamander assemblage supports earlier interpretations of the GFS as a wooded-pond environment with several feeder streams; the presence of neotenic *Ambystoma* sp. supporting the interpretation of a permanent body of water at the site.

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