The Role of the Blue Ridge Embayment in the Zoogeography of the Green Salamander, Aneides aeneus
Author(s): Richard C. Bruce
Reviewed work(s):
Source: Herpetologica, Vol. 24, No. 3 (Sep., 1968), pp. 185-194
Published by: Herpetologists' League
Stable URL: http://www.jstor.org/stable/3891010
Accessed: 30/03/2012 09:08

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp
JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of
content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms
of scholarship. For more information about JSTOR, please contact support@jstor.org.
THE ROLE OF THE BLUE RIDGE EMBAYMENT IN THE 
ZOOGEOGRAPHY OF THE GREEN SALAMANDER, 
ANEIDES AENEUS 
RICHARD C. BRUCE

The North American salamander genus Aneides of the family Plethodontidae contains five terrestrial and arboreal species restricted to the Pacific Coast region, the Rocky Mountains of south-central New Mexico, and the southern Appalachians. Its osteology and taxonomic relationships have been studied by Wake (1963). Several workers have discussed the zoogeographic history of the genus (Lowe, 1950; Gordon, 1952; Blair, 1958, 1965; Wake, 1966). The ecology of the single eastern representative, A. aeneus, has been intensively studied by Gordon (Gordon and Smith, 1949; Gordon, 1952, 1961). The present report is an attempt to analyze the zoogeography of A. aeneus, with emphasis on the Pleistocene and Recent history of the species in the southern Blue Ridge Mountains. Distributional and habitat data were taken at various times between 1962 and 1967. Although few specimens were collected, small voucher series from most localities have been deposited in the collection of the Department of Zoology, Duke University.

THE AREA

The area of study is the embayment of the Blue Ridge in western North and South Carolina and adjacent northeastern Georgia (Fig. 1). This embayment is the source of tributaries of the Keowee and Chattooga Rivers. Its northern boundary is a relatively high section of the Blue Ridge Divide, which forms an upper escarpment with major peaks between 4000 and 5000 feet above sea level. Streams draining the south slope of this escarpment flow onto a narrow plateau at about the 3400-foot level, and then at 3000 feet enter a steep lower escarpment which drops abruptly to the Piedmont some 2000 feet below. Streams have incised a series of deep gorges on the lower escarpment, and the steep gradient along which the streams descend is marked by numerous cascades and waterfalls. The major gorges are those of the Estatoe, Toxaway, Horsepasture, Thompson, Whitewater, and Chattooga Rivers.

The embayment environment is discussed by Billings and Anderson (1966). Regional climate is unique and stems directly from the physiography. The steep lower escarpment plus the encircling
mountains of the divide act as a catchment for moist air masses circulating northward from the Gulf of Mexico. Precipitation may be the highest in eastern North America, with annual means ranging from 85 to 100 inches, and perhaps exceeding 100 inches at the heads of the gorges. Temperatures are mild, indicating the existence of a thermal belt in the embayment. In the gorges temperatures are more stable than in the surrounding region.

The embayment lies within the Oak-Chestnut Forest Region (Braun, 1950). The distribution of vegetational communities, as shown in several recent studies, follows a regular pattern correlated with the topography (Cooper, 1963; Rodgers, 1965; Rodgers and Shake, 1965; Mowbray, 1966; Racine, 1966). Major communities recognized by these workers are as follows. Along the riverbanks in addition to a narrow zone of alder (Alnus serrulata), there may be a floodplain forest of various conifers and hardwoods, but usually containing Pinus virginiana, P. strobus, Tsuga canadensis, Acer rubrum, Betula lenta, Liriodendron tulipifera, and Oxydendrum arboreum. Where the floodplain is absent, i.e., where the steep gorge slopes come directly to the river edge, a riverbank community is developed consisting of such trees as Betula lenta, Liriodendron tulipifera, Magnolia fraseri, and Tsuga canadensis, and often with a dense understory of Rhododendron maximum, Leucothoe editorum, and other shrubs. The coves, ravines, and lower gorge slopes support the most diverse forests of the embayment. These can be designated mixed mesophytic and are dominated by numerous species, including Liriodendron tulipifera, Tilia hetero-
phylla, *Acer rubrum*, *Betula lenta*, *Fagus grandifolia*, *Fraxinus americana*, *Juglans cinerea*, *Magnolia fraseri*, and *Tsuga canadensis*. Various oaks and hickories are present in the mixed mesophytic forest but do not predominate. Above the mesophytic forest the intermediate-level slopes support mixed oak forest in which the canopy composition is variable, but typically includes *Quercus alba*, *Q. prinus*, *Q. rubra*, *Q. velutina*, *Q. coccinea*, *Carya glabra*, *Oxydendrum arboreum*, *Acer rubrum*, and *Liriodendron tulipifera*. Above this forest, on the drier upper slopes, the number of tree species diminishes, and the forest is dominated by *Quercus coccinea*, usually with a shrub layer of *Kalmia latifolia*. On the dry ridges and knobs oak-pine or pine forest prevails, dominated by various associations of *Quercus coccinea*, *Pinus rigida*, *P. virginiana*, *P. echinata*, and *P. pungens*.

**Distribution of *Aneides aeneus* in the Embayment**

My locality records for *A. aeneus*, together with those from the literature, are shown in Fig. 1 and listed below. Locality data were recorded from United States Geological Survey topographic maps. In some of the published accounts the information is less complete than for my localities. Some of my localities were included in an earlier checklist of the embayment herpetofauna (Bruce, 1965).

1. Pinnacle Mtn., 35°02.0'N–82°44.5'W, Pickens Co., S. C. (Brimley, 1927; Schwartz, 1954).
4. 3.3 miles by highway N Rocky Bottom, 35°04'N–82°48'W, Pickens Co., S. C. (Schwartz, 1954).
5. Toxaway Falls, S-facing slope, elev. 2700 ft, mixed pine-hardwood floodplain forest, 35°07.3'N–82°55.7'W, Transylvania Co., N. C.
7. Lower Bearcamp Falls, SW-facing slope, elev. 1200 ft, mixed mesophytic forest, 35°02.7'N–82°56.7'W, Transylvania Co., N. C.
8. Bearcamp Gorge, S-facing slope, elev. 2800 ft, mixed mesophytic forest, 35°04.2'N–82°58.1'W, Transylvania Co., N. C.
9. 0.5 mile below Windy Falls, Horsepasture Gorge, SW-facing slope, elev. 1300 ft, mixed mesophytic forest, 35°04.0'N–82°57.0'W, Transylvania Co., N. C.
10. Rainbow Falls, Horsepasture Gorge, SW-facing slope, elev. 2700–2800 ft, riverbank, mixed mesophytic, and mixed oak forest, 35°05.5'N–82°57.9'W, Transylvania Co., N. C.
11. 0.5 mile S Roundtop Mtn., SE-facing slope, elev. 3100 ft, mixed oak forest, 35°05.8'N–82°58.0'W, Transylvania Co., N. C.
12. S side Blue Ridge Divide at Hogback Mtn., S-facing slope, elev. 3500 ft, mixed oak forest, 35°07.7'N–83°00.5'W, Jackson Co., N. C.
15. Upper Thompson Gorge, W-facing slope, elev. 2400 ft, riverbank forest, 35°03.0′N–82°58.0′W, Transylvania Co., N. C.
16. 10.4 miles by highway NNW Salem, 35°00′N–83°02′W, Oconee Co., S. C. (Schwartz, 1954).
17. Upper Whitewater Falls, SE-facing slope, elev. 2600 ft, riverbank and mixed oak forest, 35°02.2′N–83°01.2′W, Jackson Co., N. C.
18. Chattooga Ridge, NE side Heady Mtn. Gap, NW-facing slope, elev. 3400 ft, mixed mesophytic forest, 35°02.5′N–83°03.6′W, Jackson Co., N. C.
19. S side Blue Ridge Divide at Zacharys Gap, S-facing slope, elev. 3900 ft, mixed oak forest, 35°08.7′N–83°04.8′W, Jackson Co., N. C.
20. Chattooga Gorge, SW-facing slope, elev. 2400 ft, mixed mesophytic forest, 35°00.8′N–83°06.7′W, Jackson Co., N. C.
21. Slick Rock, S-facing slope, elev. 3200 ft, mixed oak forest, 35°01.5′N–83°08.9′W, Macon Co., N. C.
22. Granite City, SE slope Blackrock Mtn., elev. 3100 ft, mixed mesophytic forest, 35°02.7′N–83°08.3′W, Jackson Co., N. C. (Gordon and Smith, 1949).
24. Highlands, S slope Bearpen Mtn., elev. 4100 ft, mixed mesophytic forest, 35°03.3′N–83°11.1′W, Macon Co., N. C. (Brimley, 1941; Gordon and Smith, 1949; Gordon, 1952). This locality, less than 0.5 mile north of the divide, is technically outside of the embayment. Additional localities close to the embayment are listed by Gordon (1952) and Schwartz (1954).

A. aeneus occurs throughout the embayment region from the Blue Ridge-Piedmont boundary northward to the Blue Ridge Divide, at elevations ranging from 1000 to 4400 feet. Its distribution depends on the presence of granitic rock outcrops. Specimens were observed only in narrow crevices or on the exposed surfaces of large rock masses. The microhabitats are similar to those described by Gordon (1952). Although individuals were not found in arboreal habitats, such as described by Pope (1928) in Kentucky, single specimens have been taken from arboreal situations at Highlands (Brimley, 1941) and Pinnacle Mountain (Schwartz, 1954).

Populations occur along the south slope of the Blue Ridge Divide, on the upper escarpment of the embayment, from Sassafras Mountain in the east to Satulah Mountain in the west. These can be considered high elevation populations, and one of them (Cold Mountain) represents the known upper altitudinal limit for the species. Most of the localities on the divide face to the south and support xeric plant communities. For example, the Hogback site consists of a massive south-facing rock outcrop within an upland mixed oak forest. Dominant trees are Quercus alba, Q. rubra, Q. prinus, Carya sp., Acer rubrum, and Liriodendron tulipifera; the understory consists largely of dense thickets of Kalmia latifolia. Around the outcrop itself the canopy is open, allowing sunlight to reach the rock surface. Although the Aneides crevices open to the south, the narrowness of the openings and irregularities of the walls prevent the penetration of direct sunlight. The Zacharys Gap
locality resembles that at Hogback; similar conditions apparently also prevail at Satulah Mountain (Gordon, 1952). Although neither Schwartz (1954) for Sassafras Mountain nor Eaton and Eaton (1956) for Cold Mountain described the habitats in detail, both sites are on high south-facing slopes and would be expected to support upland oak forests. The Roundtop and Slick Rock areas, both of which are on the plateau above 3000 feet in elevation, are also in mixed oak forest.

Several populations of A. aeneus, including those at Toxaway Falls, Rainbow Falls, and Upper Whitewater Falls, occur at the headwalls of the major gorges. Since each headwall is bounded by sheer rock walls or massive outcrops, great quantities of exposed rock are available for use by A. aeneus. Headwall areas provide reliable microclimates, featuring stable temperatures and high humidity (Billings and Anderson, 1966). At Rainbow Falls and Upper Whitewater Falls A. aeneus was found in outcrops immediately adjacent to the rivers in riverbank and mixed mesophytic forests, as well as in rocks on the upper slopes in mixed oak forests. These two populations seemed to be especially flourishing, with high concentrations of animals occupying extensive rocky areas. In contrast, at Toxaway Falls only a single specimen was found. It was taken from a large rock slab at the bottom of the waterfall in pine-hardwood floodplain forest. Here the gorge is less deeply entrenched and conditions are more xeric than at the other headwall localities.

Most of the remaining sites for which adequate observations are available can be characterized as mesic, occurring within riverbank and mixed mesophytic forest communities at both high and low elevations. The Granite City and Highlands populations studied by Gordon (1952) are in mixed mesophytic communities above 3000 feet in elevation, as is the population at Heady Mountain Gap. Most known populations of A. aeneus at lower elevations of the embayment occur in mesic forests within the gorges proper, either in outcrops of rock on slopes adjacent to the major streams (e.g., Lower Bearcamp Falls, Windy Falls, Upper Thompson Gorge, Chattooga Gorge), or in rocky areas of adjacent coves (e.g., Bearcamp Gorge). All of these localities are humid and heavily shaded, although forest conditions vary from site to site. For example, the Chattooga Gorge locality consists of several granite outcrops on a steep slope about 100 feet above river level. Near the rocks the forest is dominated by mature hemlocks (Tsuga canadensis); consequently very little sunlight penetrates to the forest floor. In contrast, in the Upper Thompson Gorge populations of A. aeneus were in riverbank forest adjacent to the river. Here a dark and humid environment is provided by dense tangles of Rhododendron maximum which surround the outcrops.
The available information on the local distribution of *A. aeneus* in the embayment suggests the following conclusions. On the upper escarpment and plateau the species occurs in a variety of xeric and mesic forest communities. On the lower escarpment populations are concentrated in the mesic forests of the gorges, rather than on adjacent peaks and ridges. This may reflect the abundance of rock habitats on the steep lower slopes of the gorges; however, it may also indicate that the exposed upper slopes and ridgetops of the lower escarpment are subject to climatic extremes unsuitable for the species. Gorges with moderate temperatures and high precipitation show a climatic stability which cannot be duplicated within the present geographic range of *A. aeneus*. Since this stability has existed through Pleistocene and Recent times, the escarpment gorges have probably provided *A. aeneus* with reliable microclimates during the disruptive climatic events of the Quaternary Period. Thus the embayment region as a whole, but particularly the gorges of the lower escarpment, can be regarded as a potential refugium for *A. aeneus* (and perhaps other salamander species) during periods of widespread climatic change.

**Zoogeographic History of Aneides aeneus**

Deevey (1949) expressed the hypothesis that the Plethodontidae is a young family in which the majority of species and even many genera originated as recently as the Pleistocene, and further that the geographic pattern of distribution within the family is the result of Pleistocene and Recent events. His primary example, admittedly speculative, is an attempted demonstration of Pleistocene speciation within the genus *Plethodon*; however, his argument has been weakened by recent taxonomic work on the genus (Highton, 1962). A serious objection to Deevey's hypothesis is his implication that the timetable of events suggested for *Plethodon* is applicable to other genera of plethodontids. The family as a whole appears to be much older than the Pleistocene, and many of the existing North American genera may have originated in early Tertiary times (Wake, 1966). Undoubtedly Pleistocene and Recent climatic changes produced shifts in distribution which may have precipitated taxonomic differentiation (Smith, 1957; Conant, 1960). However, these Quaternary events did not necessarily obliterate the broader features of pre-existing patterns of distribution, and many aspects of the present zoogeography of the plethodontids must be interpreted in the light of Tertiary history.

For the genus *Aneides* the present geographic distribution is a relict pattern which apparently has been derived from an earlier (mid-Tertiary) transcontinental distribution. Lowe (1950) believed that fragmentation of the range occurred in late Miocene-
early Pliocene times. Subsequent workers have supported and elaborated upon this hypothesis (Gordon, 1952; Wake, 1966). Blair (1958, 1965) has suggested that Rocky Mountain and eastern elements of the genus may have been in contact as recently as the late Pleistocene. Wake (1966) has argued convincingly against this viewpoint, and should be consulted for a general assessment of the biogeographical history of the genus.

The present geographic range of A. aeneus, as mapped by Gordon (1952, 1967), consists of two sections, separated by the Appalachian Valley. The more extensive western section is mainly within the Appalachian Plateau Province from southwestern Pennsylvania to central Alabama; the more restricted southeastern section is centered around the Blue Ridge embayment. The distribution of A. aeneus in the Appalachian Plateau is largely coincident with the Mixed Mesophytic Forest Region; even in the Southern Blue Ridge the species occurs for the most part in mixed mesophytic communities or in areas containing such communities as important constituents of the vegetational complex. According to Braun (1950) and others (Monk, 1967) the mixed mesophytic association is the most diverse component of the Eastern Deciduous Forest, and is the least differentiated remnant of the Arcto-Tertiary Forest which spanned the continent in the Tertiary Period. It has been postulated that the Tertiary distribution of Aneides coincided with this forest, and that A. aeneus is a relict which has maintained the old association with mixed mesophytic forest (Lowe, 1950; Gordon, 1952; Wake, 1966). Although this hypothesis may be essentially correct, it does not take into account the possible effects of later (Pleistocene and Recent) climatic changes on the distributional pattern. Most contemporary investigators have concluded that during the Pleistocene the southeastern United States was subjected to at least moderate cooling accompanied by considerable shifts in plant distributions at the times of glacial advances (Dillon, 1956; Whitehead, 1964, 1965).

Two ecological factors need to be recognized in any hypothesis of the zoogeography of A. aeneus. First, the morphological characteristics and habitat features of the genus indicate an evolutionary trend from a ground-dwelling to an arboreal mode of life (Wake, 1963, 1966). As Gordon (1952) has noted, the utilization of arboreal habitats by A. aeneus is largely restricted to the area of maximum development of mixed mesophytic forest within the Appalachian Plateau Province. In other areas the species is primarily an inhabitant of rock crevices. Since these crevices provide a unique microclimate which may be quite different from the general climate of the surrounding forest (Gordon, 1952), adaptation to crevice habitats seemingly would have freed A. aeneus from dependence on a specific forest community. However, its ability to occupy ter-
restrial and arboreal habitats may still be restricted to mixed mesophytic situations. Thus, whereas *A. aeneus* may potentially be able to live in rock crevices outside of the mixed mesophytic forest, the necessity of dispersal across the forest floor may be responsible for its limited incursion into other areas. A second ecological factor concerns the reproductive habits. In the southern Blue Ridge the eggs of *A. aeneus* are deposited in early summer and undergo a long incubation period (about 3 months), during which time they are brooded by the female (Gordon, 1952). This restriction of female activity in the warmer months of the annual cycle may explain the absence of the species at elevations above 4400 feet in the southern mountains (Gordon, 1967).

With these various factors taken into consideration I propose the following hypothesis. By late Pliocene times *A. aeneus*, or populations ancestral to it, became confined to the Appalachian Plateau and Blue Ridge Provinces. This restriction may have been coincident with the Harrisburg erosion cycle and the concomitant segregation of plant communities in the Southeast (Braun, 1950). Later, during the recurring glaciations of the Pleistocene, the range of the species undoubtedly fluctuated, but probably not far beyond the limits of mixed mesophytic forests. At the time of the most recent glacial advance *A. aeneus* withdrew into southern refugia – one in the southern part of the Appalachian Plateau Province, the other in the Blue Ridge embayment region. With the retreat of the glaciers and amelioration of the climate the species dispersed from its western refugium northward through the relatively low elevations of the Cumberland and Alleghany plateaus. A corresponding dispersal from the southeastern refugium has not occurred. It would appear that the Blue Ridge region to the north of the embayment is a formidable barrier to *A. aeneus*. Elevations in excess of 5000 feet are common in many of the ranges, and the rugged and irregular topography does not provide natural avenues of dispersal. Thus the present distribution along the southern edge of the Blue Ridge may essentially represent the range of the species at the time of the Wisconsin glacial maximum. The survival of *A. aeneus* in the southern Blue Ridge is likely a consequence of continuously stable microclimates in the escarpment gorges of the embayment and in other low elevation gorges of the surrounding region.

**Acknowledgments**

Preliminary field work for this study was supported by NSF G-17005 awarded to the Highlands Biological Station. The study was completed during my tenure at Duke University as an NSF Science Faculty Fellow. I wish to thank Dr. Joseph R. Bailey for his critical assessment of the manuscript. Thanks are also due Mr. W. Earl Sipe for able assistance in the field.
LITERATURE CITED


One of the most time consuming chores of the student of Neotropical amphibians is the determination of many of the names proposed in the Nineteenth Century. In most cases, the type specimens were inadequately described, and in many cases the provenance of the types was given only in vague sometimes erroneous terms. Proper determination of such names often is possible only after gaining a thorough knowledge of a group and careful comparison of the types with series of fresh specimens.

The purpose of the present paper is to provide evidence for the proper allocation of five nominal species of *Hyla: cadaverina* Cope, 1866; *coriacea* Peters, 1867; *mocquardi* Günther, 1901; *plicata* Brocchi, 1877; and *spinosa* Steindachner, 1864. In addition the taxonomic relationships of the two nominal species of *Diaglena* are discussed.

For the loan of specimens, I am grateful to Josef Eiselt, Naturhistorisches Museum, Wien (NMW); Jean Guibe, Musée National d'Histoire Naturelle, Paris (MNHN); Alice G. C. Grandison, British Museum (Natural History) (BMNH); Edmond Malnate, Academy of Natural Sciences of Philadelphia (ANSP); James A. Peters,