

SIZE AND ALTITUDE CORRELATION IN THE GREEN
SALAMANDER, ANEIDES AENEUS

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An Abstract
Presented to the
Graduate and Research Council
Austin Peay State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Biology

by
Amy Dolores Atkins
June, 1988

ABSTRACT

A study was conducted to determine if populations of the green salamander, Aneides aeneus, from the southern Appalachian Mountains of North and South Carolina, show size variation that correlates with change in altitude.

Statistical analysis of a sample of 187 adults collected at elevations ranging from 488 to 1341 meters showed a significant increase in size with an increase in altitude.

An analysis of 37 hatchlings from the same geographic region was also made to determine if observed size differences varied altitudinally. No significant correlation was found.

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To the Graduate and Research Council:

I am submitting herewith a thesis written by Amy Dolores Atkins entitled "Size and Altitude Correlation in the Green Salamander, Aneides aeneus." I have examined the final copy of this paper for form and content, and I recommend that it be accepted in partial fulfillment of the requirements for the degree Master of Science, with a major in Biology.

David Snyder
Major Professor

We have read this
thesis and recommend
its acceptance:

Edward A. Chute
Second Committee Member

A. Floyd Scott
Third Committee Member

Accepted for the Graduate
and Research Council:

William H. Ellis
Dean of the Graduate School

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CHAPTER I
INTRODUCTION

Geographic variation, the occurrence of morphological differences among spatially segregated populations of a species, is a nearly universal phenomenon in the animal kingdom. Size is the character generally considered to be most subject to geographic variation (Mayr 1963). In fact, Mayr states that size varies in virtually every species that has an extensive range with variable climates. Because climatic factors generally change rather slowly over wide areas, they often result in variability which is expressed in regular gradients.

One form of geographic variation in size is described by Bergmann's Rule, which states that geographic races of a species are usually larger in cooler than in warmer latitudes (Lindsey 1960). Mayr (1963) states that Bergmann's Rule also tends to be valid for changes of size with altitude; although he does not mention temperature in connection with altitude, these size changes are probably another effect of temperature change. This rule is generally applied to homeotherms, but may also apply to poikilotherms.

The objectives of this study were: 1) to review the

available literature on the applicability of Bergmann's Rule to poikilothermic vertebrates; 2) to determine if a significant correlation between size and altitude exists in a sample of adult green salamanders, Aneides aeneus, taken from various elevations in the southern Appalachian Mountains in western North and South Carolina; and 3) to determine if a sample of hatchling Aneides aeneus from the same population shows any correlation between body size and altitude.

CHAPTER II
LITERATURE REVIEW

Many studies have concerned geographic variation in animals, but few have dealt specifically with poikilotherms and size variation as it relates to altitude.

Size Variation with Latitude or Temperature

A large number of the studies have addressed variation in body size of poikilothermic species in relation to latitude or temperature. Tinkle (1961) reported that Sternothaerus odoratus from northern populations averaged larger than those from southern populations. Bullock (1955) stated that northern races of species are "generally larger." Lindsey (1960), in an interspecific study, found that members of the family Plethodontidae show the size-latitude trend very sharply over their New World ranges. The experimental and field observations of Gunn (1942) and Wimpenny (1941) noted that clines for increasing size are correlated with decreasing environmental temperature gradients in many poikilotherms.

Ray (1960) reported Bergmann's Rule as valid when applied to thirteen of the seventeen poikilothermic species studied in his experiments. Those species represented one plant phylum, four invertebrate phyla (six classes), and two vertebrate classes. Two species

of amphibians were included (Bufo boreas and Rana sylvatica). All of these species exhibited size variation inversely correlated with temperature. Ray concluded that body length may be from ten to fifty percent larger for a 10°C decrease in temperature and that there were no known cases in which there was a reversal of the rule. In fact, Ray felt that with more work on the species that were exceptions, the three-fourths figure would likely go even higher. He concluded that Bergmann's Rule applies equally to poikilotherms and homeotherms.

Several studies have reported on responses of amphibians to differing temperatures approximating latitudinal or altitudinal differences. Ray (1960) studied two species of anurans and found that Bufo boreas exhibited a smooth gradient from smaller sizes at higher temperatures to larger sizes at lower temperatures. Rana sylvatica showed a similar trend.

Uhlenhuth (1921) studied three species of Ambystoma (maculatum, opacum, and tigrinum) which differed in body length by 13.3, 17.6, and 16.7 percent, respectively, when reared at temperatures of 15°C and 25°C .

In other studies reporting correlations between size and temperature, Imai (1937, cited by Ray 1960), in his work on Drosophila melanogaster, observed that larvae were 9.9 percent larger when reared at 18°C than when reared at 28°C . MacArthur and Baillie (1929) noted

that Daphnia magna were 45.9 percent larger at 18°C than at 28°C. In Crenobia, Whitney (1942) found a maximum length 183.4 percent larger at 7-8°C than at 12-13°C. Coker (1933, cited by Ray 1960) stated that Cyclops vernalis males were 29.8 percent larger and females 45.9 percent larger at 7-10°C than at 29-30°C. Imai (1937, cited by Ray 1960) recorded that Lymnaea japonica, when reared at 10°C and 20°C, showed a 7.8 to 12 percent body length increase at the lower temperature. Hall (1925) found the fry of Coregonus were 20.9 to 67.5 percent larger at low temperatures.

Variation with Altitude

The studies cited concerned size variation with latitude or temperature. While variation with altitude has not been as extensively documented, several studies have addressed this topic with respect to both homeotherms and poikilotherms.

Homeotherms. Hairston (1949) reported that size clines are common among birds, "especially on mountainsides." Ray (1960), in his review, found that an "overwhelming majority" of birds and mammals studied exhibited an altitudinal size cline in conformity to Bergmann's Rule.

Poikilotherms. Studies have shown that poikilothermic species can exhibit similar variation with altitude. This variation may involve morphology, color pattern, or size, among others.

Ruibal (1955) recorded variation in morphology among Rana pipiens from various elevations, and in a later study (1957) reported that snout shape of the same species showed an altitudinal cline. Tilley (1969) found variation in color pattern of Desmognathus ochrophaeus from different altitudes. Gordon (1967) stated that intensity of pigmentation varies with altitude in Aneides aeneus. Pettus and Spencer (1964) noted that the greatest contrast between Pseudacris triseriata populations from different elevations was in body size, which showed a trend of smaller to larger from lower to higher elevations. A similar size cline in Pseudacris triseriata was reported by Miller and Packard (1977). Montane populations of Rana clamitans were found to be consistently larger than those from lowlands (Berven et al. 1979).

Beckenbach (1975) noted a positive correlation between body size and elevation among species of neotropical salamanders. Hairston (1949) found a gradual but definite trend of increasing size with increasing altitude in populations of Desmognathus ochrophaeus carolinensis. He also reported that specimens from higher elevations seemed darker in color than those from lower elevations. Dunn (1928) stated that dark color is correlated with large size in this species.

Desmognathus ochrophaeus was also studied by Martof

and Rose (1963), who reported that males from an elevation of 950 feet had an average snout-vent length of 28 mm while those from 6450 feet averaged 49 mm. Females also were larger at higher elevations (27 mm at the lowest elevation compared to 45 mm at the highest).

Tilley (1973) showed that Desmognathus ochrophaeus increased in size from 39 mm at 914 feet altitude to 48 mm at 1981 feet. In a second study Tilley (1974) again found that high-altitude populations of D. ochrophaeus attained larger size.

Desmognathus quadramaculatus has also been found to show variation in size with altitude. Hairston (1949) reported differences in size that he suspected may have been significant, but his series was not large enough to demonstrate the difference statistically.

Bruce (1972) reported that larger body sizes are attained by Gyrinophilus porphyriticus at higher elevations.

In a study of Ambystoma macrodactylum, Kezer and Farmer (1955) found that populations below 5500 feet were from 60 to 80 mm in total body size, while those above 6000 feet were 70 to 90 mm.

The preceding studies demonstrated altitudinal variation in several species of amphibians, but I could find no such studies dealing specifically with Aneides aeneus. Gordon (1952), in his life history of this species, noted that this sort of study was needed.

All studies mentioned support the idea that Bergmann's Rule is applicable to poikilotherms, but a few studies contest this conclusion. Masaki (1967) reported that "no principle comparable to Bergmann's Rule for warm-blooded animals has been established for insects." His study of Emma field crickets found that body size tended to become smaller from low to high altitudes. Feder et al. (1982) found no significant correlation between body size and elevation among species of tropical salamanders of the genus Bolitoglossa.

Head Width.

I found no studies correlating head width with altitude. Brodie (1970) found geographic variation in head width of Plethodon dunnii and P. elongatus. Head width does generally increase with other measures of increasing body size, which may be why it is seldom considered separately.

Hatchling Size Variation

I found only one study that mentioned variation of hatchling size as a function of elevation. Danstedt (1975) found no difference in hatchling size of Desmognathus fuscus in a sample representing six populations from altitudes between 46 m and 671 m, though his sample consisted of an unspecified number of specimens.

CHAPTER III
METHODS AND MATERIALS

My sample consisted of 187 adult and 37 hatchling Aneides aeneus, collected from May to September of 1970 at elevations ranging from 488 to 1341 meters. Samples were collected by David H. Snyder from different sites in Jackson, Macon, and Transylvania counties, North Carolina, and Oconee County, South Carolina (see appendix for description of sites). The specimens were preserved in 10 percent formalin until transferred to 70 percent ethanol in 1986 (just before I measured them).

Snout-vent length and head width were measured to the nearest 0.1 mm with a vernier caliper. All measurements were taken twice to ensure accuracy. Snout-vent length was measured from the tip of the snout to the anterior end of the cloacal aperture. Head width was measured across the widest part of the head, which was the muscular area just posterior to the eyes.

Adults were sexed and separated by examining gonads. Maturity was assessed by gonadal inspection as well. Levels of maturity were double-checked using Gordon's (1969) findings that sexually mature males are minimally 42 mm in snout-vent length, and females minimally 46 mm. He considered all individuals below those limits immature, and visual inspection of the

gonads of my sample confirmed the validity of his conclusion. Only mature individuals were included in the statistical analysis.

The Monroe program for Duncan's Multiple Range Test (Bruning and Kintz 1968) was used to determine if significant differences existed between the snout-vent length of either adult males and females at each elevation, or between males and females from all elevations. No significant differences were revealed, therefore males and females from each elevation were combined to provide a larger sample.

Pearson's correlation coefficient was determined using the SPSS-X computer program. Correlation of snout-vent length with altitude, and head width with altitude, were considered for adults and for hatchlings. Regression coefficients for these pairs of variables were also calculated.

CHAPTER IV

RESULTS

Adults

Mean snout-vent length, range, and confidence limits of the means for each population are presented as a Dice-gram in Figure 1. The correlation analysis comparing snout-vent measurements with elevations gave a product-moment correlation coefficient of 0.2, with a P value of 0.007. The regression equation of snout-vent length on elevation was $y = 52.8 + 0.004x$.

The Dice-gram in Figure 2 shows the mean, range, and confidence limits of the head widths from each elevation. The product-moment correlation coefficient for head width versus elevation is 0.22, with a P value of 0.002. The regression equation is $y = 7.9 + 0.003x$.

Hatchlings

The analysis of the data on hatchlings revealed no significant correlation between snout-vent length and elevation.

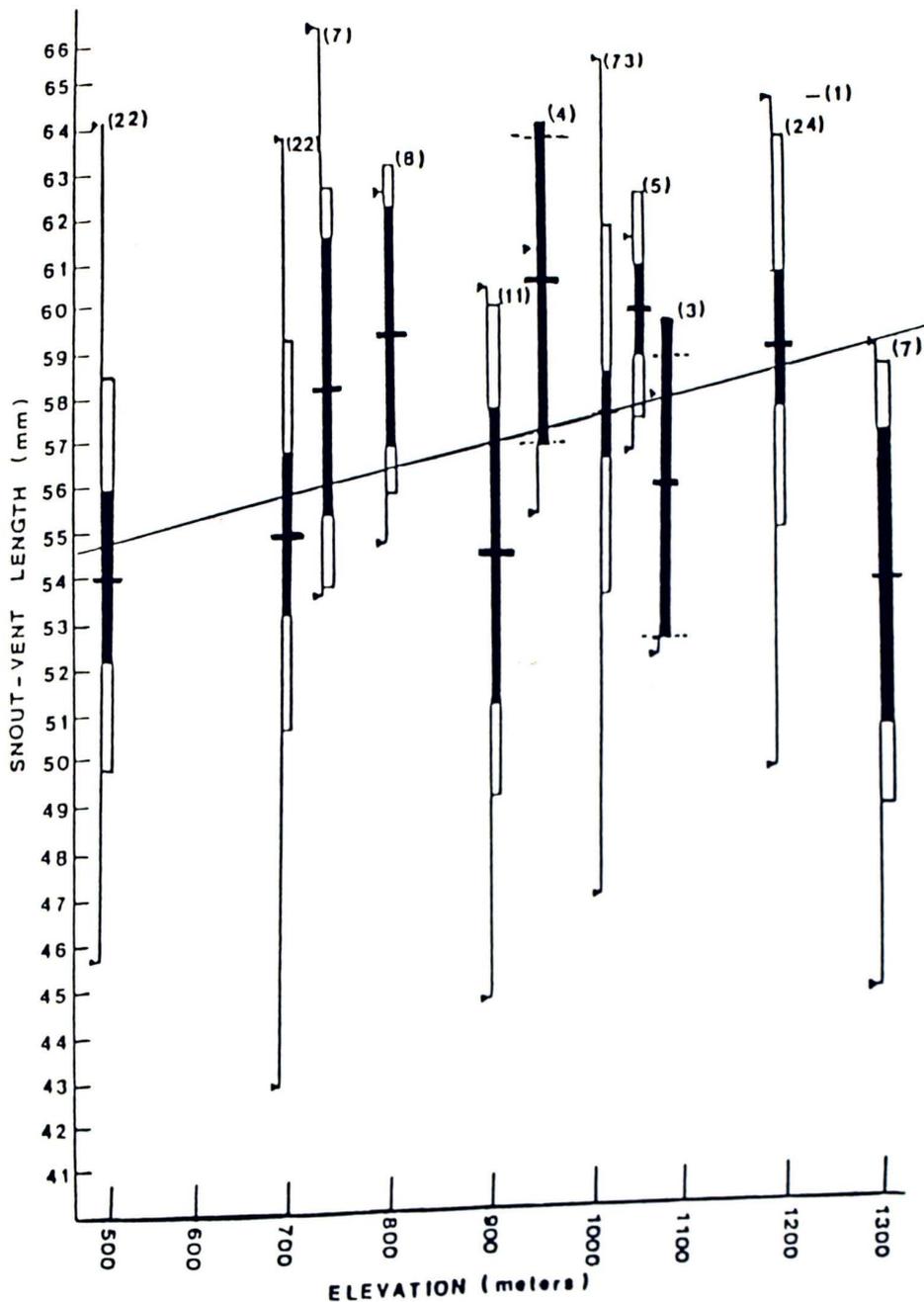


Figure 1. Variation in snout-vent length for samples of adult *Aneides aeneus* from different elevations in North and South Carolina. The short horizontal line indicates the sample mean; the vertical line between solid triangles the range of variation; the dark boxes, twice the standard error of the mean on each side of the mean; and the open boxes plus the dark boxes one standard deviation on each side of the mean. Broken horizontal lines indicate limits of open boxes in instances where two times the standard error of the mean exceeds one standard deviation. Sample sizes are in parentheses. The regression line is also shown.

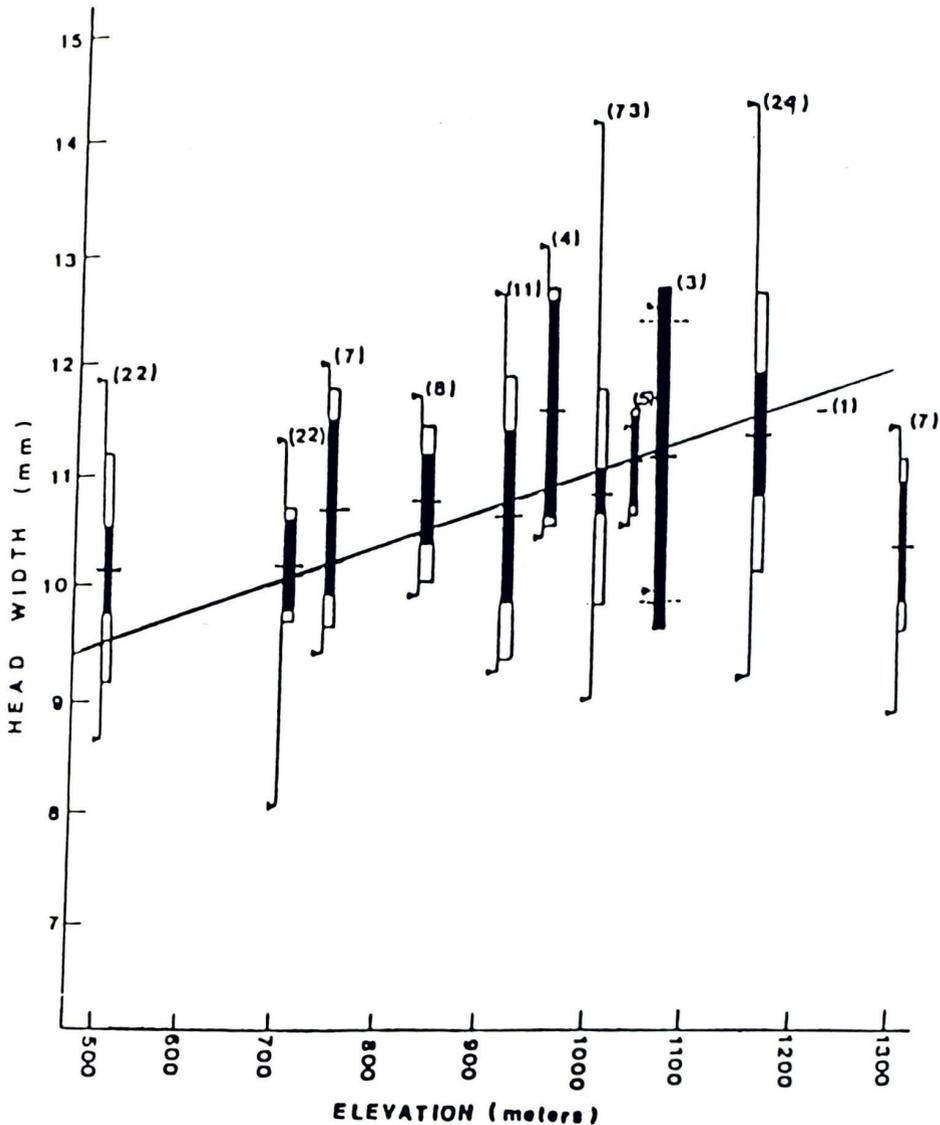


Figure 2. Variation in head width for samples of adult *Aneides aeneus* from different elevations in North and South Carolina. The short horizontal line indicates the sample mean; the vertical line between solid triangles the range of variation; the dark boxes, twice the standard error of the mean on each side of the mean; and the open boxes plus the dark boxes one standard deviation on each side of the mean. Broken horizontal lines indicate limits of open boxes in instances where two times the standard error of the mean exceeds one standard deviation. Sample sizes are in parentheses. The regression line is also shown.

CHAPTER V

DISCUSSION AND CONCLUSIONS

I combined data from adult males and females to provide larger samples from each elevation, since no significant difference was found between size of males and females at each altitude, or between size of all males and size of all females.

Although visual examination of Figure 1 does not suggest a definite trend toward increased body length with increased altitude, the product-moment correlation coefficient (r) of 0.2 between snout-vent length and elevation was significant at the one percent level of confidence. This confirms a positive correlation between size and altitude.

Figure 2 suggests a slight trend toward increased head width with increased elevation and the statistical analysis confirms this trend to be significant. The product-moment correlation coefficient of 0.22 is significant at the one percent confidence level.

This statistical analysis revealed a significant correlation between altitude and two measures of body size (snout-vent length and head width) of the adult salamanders in this study. Other authors also reported increases in body size with an increase in elevation in Pseudacris triseriata (Pettus and Spencer 1964), Rana clamitans (Berven et al. 1979), Desmognathus ochrophaeus

(Hairston 1949, Martof and Rose 1963, Tilley 1973), Desmognathus quadramaculatus (Hairston 1949), Gyrinophilus porphyriticus (Bruce 1972), and Ambystoma macrodactylum (Kezer and Farmer 1955). The findings in my study can also be compared with studies which found increased size with decreased habitat temperature. Studies involving size and temperature can be compared to studies on size and altitude because, as Hairston (1949) explains, "the most obvious difference between high and low elevations is in temperature. Chapman's Rule states that there is a drop of 1°C for each 540 feet of elevation gained." Studies on size-change with latitude can also be compared to my study because temperature varies similarly with altitude and latitude. While temperature definitely does vary with altitude and latitude, it is not, as Ruibal (1957) states, "the only environmental factor" to do so. Rainfall, vegetation, and prey availability are a few factors which also vary.

The altitudinal range represented in this study was from 488 to 1341 meters; the latter elevation is the known upper altitudinal limit for Aneides aeneus (Bruce 1968). This range was sufficient to produce appreciable differences in temperature, with temperatures averaging higher at lower sites (Snyder 1971). The temperature at the highest altitude should have averaged 5° less than at the lowest altitude according to Chapman's Rule.

There could be many reasons why size increases at higher elevations. The two most prevalent explanations concern heat conservation and oxygen consumption. Bergmann's Rule has often been interpreted as having significance in terms of metabolic heat (Mayr 1942, Wimpenny 1941, McNab 1971). Of course, with poikilotherms it is improbable that heat conservation is an important factor, but as Ray (1960) pointed out, the rule actually says nothing about heat conservation.

Beckenbach (1975), Feder (1983), Gunn (1942), and Whitford and Hutchison (1967) all state that larger animals consume less oxygen per unit weight, and more efficiently utilize the less-available oxygen at higher elevations. Beckenbach (1975) explains that respiratory limitations are the primary factors leading to the latitudinal and altitudinal size clines observed in plethodontids.

Bruce (1972) offered yet another correlation for larger size at higher elevations. He found that low-elevation populations of Gyrinophilus porphyriticus were characterized by early maturity and small size, whereas high elevation populations showed larger body size as a consequence of delay in development.

These are only two possible explanations of why individuals of a species are larger at higher than at lower elevations. Other unrecognized factors might also explain this variation.

One objective of my study was to determine if newly hatched Aneides aeneus showed a correlation between size and altitude similar to that found in adults. I found only one previous study which addressed the question of variation in hatchling size with elevation. Danstedt (1975) found no such variation in Desmognathus fuscus from altitudes between 46 meters and 671 meters. The results of my study also show no significant correlation between hatchling size (either snout-vent length or head width) and altitude, though my sample sizes were small and few elevations were represented.

CHAPTER VI

SUMMARY

I statistically analyzed data from 187 adult Aneides aeneus from twelve elevations (from 488 to 1341 meters) and found a significant positive correlation, at the one percent level of confidence, between body size and elevation. This finding agrees with the results of several other studies which report that Bergmann's Rule is applicable to poikilotherms as well as to homeotherms.

Analysis of data from a small sample of hatchlings (37 individuals) from some of the same populations revealed no significant correlation between size and altitude.

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APPENDIX 1

Description of Collection Sites
(Taken from Snyder 1971)

- 488 meters. Lower Whitewater Falls. South Carolina, Oconee County. Northeast and southwest banks of the Whitewater River at foot of falls. Riverbank and mixed mesophytic forest. Reid Quadrangle.
- 701 meters. Upper Whitewater Falls. North Carolina, Jackson County. Southwest bank of Whitewater River, about 0.1 mile below foot of falls. Mixed mesophytic forest. Cashiers Quadrangle.
- 732 meters. Chattooga Gorge. North Carolina, Jackson County, Northeast bank of Chattooga River. Mixed mesophytic forest. Cashiers Quadrangle.
- 823 meters. Chattooga Cliffs. North Carolina, Jackson County. East bank of Chattooga River at confluence of Cane Creek. 1 mile north of Bullpen Road bridge. Mixed mesophytic forest. Highlands Quadrangle.
- 914 meters. Roundtop Mountain. North Carolina, Transylvania County. Southeast slope of southern spur of Roundtop Mountain. Mixed oak forest. Reid Quadrangle.
- 945 meters. Wilson Gap Road. North Carolina, Macon County. Northeast slope of Little Fodderstack Mountain, 0.3 miles south of Bullpen Road. Mixed mesophytic forest. Highlands Quadrangle.
- 1006 meters. Round Mountain. North Carolina, Jackson County. Southwest bank of Whitewater River, northeast slope of Flat Mountain. Mixed mesophytic forest. Cashiers Quadrangle.
- 1036 meters. Heady Mountain Gap. North Carolina, Jackson County. Northeast side of Heady Mountain Gap on Chattooga Ridge. West-southwest facing slope. Mixed mesophytic forest. Cashiers Quadrangle.
- 1067 meters. Hogback Mountain. North Carolina, Jackson County. South slope of Hogback Mountain, southwest facing slope. Mixed oak forest. Big Ridge Quadrangle.
- 1189 meters. Rhododendron Trail. North Carolina, Macon County. Highlands Biological Station. South slope of Bearpen Mountain. Mixed mesophytic forest. Highlands Quadrangle.

1219 meters. Sassafras Knob. North Carolina, Macon County. Northwest slope of Sassafras Knob. Extreme southwest corner of Highlands. Mixed oak forest. Highlands Quadrangle.

1341 meters. Cold Mountain. North Carolina, Transylvania County. Within a few hundred feet of Jackson County line. 5 miles west of Lake Toxaway. Bare cliffs. Reid Quadrangle.