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The Influence of Habitat Variation on the Morphology and Physiology of *Plethodon Wehrlei* (Fowler and Dunn) in West Virginia

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THE INFLUENCE OF HABITAT VARIATION ON THE
MORPHOLOGY AND PHYSIOLOGY OF PLETHODON
WEHRLEI (FOWLER AND DUNN) IN WEST VIRGINIA

A Thesis
Presented to
the Faculty of the Graduate School
of Marshall University

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

by
Sharon Kay Gross
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as meeting the research requirement for the master's degree.

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ABSTRACT

High elevation, low elevation and cave populations of Plethodon wehrlei (Fowler and Dunn) in West Virginia were compared to determine the influence of habitat variation on morphology and physiology. Discriminant analysis of 14 external morphological characters and 11 skeletal characters revealed a similar morphology for the three populations. Comparisons of critical thermal maxima showed a positive correlation to habitat temperature. Dehydration studies revealed that the high elevation population was more resistant and tolerant to water loss than the cave and low elevation populations.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Wehrle's salamander, Plethodon wehrlei (Fowler and Dunn, 1917), is a relatively large woodland species belonging to the family Plethodontidae. This family is unique among other families of salamanders in that it lacks lungs (respiration is accomplished through the integument and the lining of the mouth) and has naso-labial grooves (cutaneous depressions which extend from each nostril to the edge of the mouth and function in detecting chemical cues from the substrate). P. wehrlei exhibits a dorsal color of black or dark brown with whitish flecks found only along the sides. The belly is gray and the throat is off-white with gray flecks (Fig. 1). It attains a maximum length of 152 mm with a modal number of 17 costal grooves (Highton, 1971). Juveniles in the southern portion of the range often have rows of red or orange spots on the back. P. wehrlei ranges from extreme southwestern New York to central Virginia (Conant, 1975) (Fig. 2). Within the mixed deciduous forest, a wide variety of habitats are utilized: beneath logs and stones, in rock crevices and in twilight zones of caves (Conant, 1975). Food habits of P. wehrlei indicate that a variety of prey is utilized. Pauley (1978a) found that P. wehrlei in Doddridge County, West Virginia feeds mainly on ants (Formicidae), mites (Acaria) and beetles (Coleoptera). Hall (1976) found similar feeding habits in a population from Tioga County, Pennsylvania.

Hall and Stafford (1972) found that the life cycle of P. wehrlei is similar to that of the slimy salamander, P. glutinosus (Highton, 1956, 1962). Hall and Stafford (1972) found that P. wehrlei in Pennsylvania lay eggs in mid-winter or early spring whereas Pauley

Figure 1. Plethodon wehrlei; dorsal and ventral views of adult female.



Figure 2. Range of Plethodon wehrlei.



and England (1969) reported that egg laying occurs in May or June in West Virginia, 200 miles south. Hall and Stafford also found that the Pennsylvania population appears to exhibit a longer period of growth and greater average size than the southern populations. Pauley (1978b,c,d) examined the microdistribution of sympatric populations of P. wehrlei and P. cinereus in Doddridge County, West Virginia. He found P. wehrlei to be more abundant in areas with understories of red maple-sourwood and a ground cover of shrubs whereas P. cinereus was more abundant in areas with understories of sugar maple-beech and a ground cover of herbs. He also found P. wehrlei active at warmer soil temperatures (higher cloacal temperatures) and more tolerant to high experimental temperatures (higher CTM) compared to P. cinereus. P. wehrlei has also been shown to survive dryer conditions than P. cinereus (Pauley, 1978d). Other than the results of these studies, little is known about the ecology and geographic variation of P. wehrlei. Hall and Stafford (1972) suggested that this may be due to the fact that it is apparently rare throughout most of its range.

Unlike other woodland salamanders, P. wehrlei frequently inhabits caves and some populations appear to be restricted to cave habitats. In a survey of salamanders found in West Virginia caverns, Green and Brant (1967) listed six caves (three counties) in which P. wehrlei was found. Barr (1967) classifies the fauna of caves into four groups; troglobites, troglaphiles, troglaxenes or accidentals. Troglobites are the true obligatory cave dwellers which are unable to survive except in caves. Troglaphiles are facultative cave dwellers which are commonly found in caves and are capable of completing their life cycles there, but are also found in epigeal environments. Troglaxenes are animals

which utilize the cave for shelter and a favorable habitat but must return to the surface for food. Accidentals include those animals which wander in or are washed in during floods. Green and Brant (1967) stated that P. wehrlei might be a troglaxene. In another study, Clerque-Gazeau (1974) considered P. wehrlei a troglaxene, although her definition is somewhat different from Barr's in that food in the cave is also utilized. From data collected over the last fifty years, it is apparent that a population of P. wehrlei has thrived in at least one cave in West Virginia. P. wehrlei has been collected from McClung's Cave, Greenbrier County, West Virginia, numerous times over the last fifty years indicating a strong population is maintained there. Other than incidence of occurrence (Cooper, 1960, 1961; Green and Brant, 1967), no research has been reported on cave populations of P. wehrlei. Netting (1936) examined specimens of P. wehrlei from Arbuckle's Cave, Greenbrier County, and concluded that its morphology was somewhat atypical and showed a resemblance to P. glutinosus. He suggested that these cave specimens may have been affected by the habitat.

Studies on woodland populations of P. wehrlei (Hall and Stafford, 1972; Hall, 1976; Pauley, 1978a,b,c,d) have been in regions of relatively low elevation (< 762 m). Museum records, however, show that P. wehrlei ranges up to elevations of 1474 m in Pochahontas County, West Virginia. Wehrle's salamander offers an excellent model for examining intraspecific ecological divergence because it inhabits such a broad diversity of habitats in West Virginia.

Interspecific variation in morphology and physiology has been examined for many salamander species. Wake (1966) conducted an extensive study of comparative osteology in the family Plethodontidae.

Brandon (1971) examined interspecific variation in cave dwelling salamanders and defined features which he considered adaptive to the cave habitat. Analyses of critical thermal maxima (CTM) have repeatedly shown interspecific variation associated with habitat and acclimation (Zweifel, 1957; Hutchinson, 1961; Sealander and West, 1969; Spotila, 1972) but only rarely, has variation been shown within species (Hutchinson, 1961; Spotila, 1972). Evaporative water loss studies have demonstrated positive correlations between species' rates of water loss and moisture conditions of their natural habitats (Thorson, 1955; Ray, 1958; Hutchinson, 1958; Pauley, 1978b). Little work, however, has been done on variation of water loss rates within a species.

The objective of the present study on P. wehrlei was to analyze variations in rates of water loss, heat tolerance, and general morphology which might indicate intraspecific adaptations or acclimation to cave, montane and low elevation habitats. Examination of morphological and physiological divergence within a species may provide greater insight on the immediate effect these habitats have on a salamander's ecology.

CHAPTER II
MATERIALS AND METHODS

Fifteen external morphological characters were measured on 232 museum specimens of Plethodon wehrlei collected in West Virginia (Appendix 1). Specimens were grouped into three geographical populations: (1) low elevation (82 specimens) in Mason, Taylor, Doddridge and Harrison Counties (183-366 m); (2) twilight zones of caves (50) in Greenbrier County (640-671 m); and (3) high elevations (100) in Pocahontas, Randolph, Pendleton and Tucker Counties (931-1474 m) (Fig. 3). Measurements to the nearest tenth of a millimeter were made with a Helios vernier caliper. Only specimens with snout-vent lengths greater than 37 mm were measured in the analysis in accordance with Hall and Stafford's (1972) designation of adult size in P. wehrlei. Characters measured were: eye diameter (ED), head length (HL), head width (HW), head depth (HD), snout length (SL), snout width (SW), snout depth (SD), snout-vent length (SV), body length (BL), humerus length (Hu), radius and ulna length (RU), femur length (Fe), tibia and fibula length (TF), and gular fold width (GF) (Figs. 4 and 5). Costal groove count (CG) was also recorded.

Twelve skeletal characters were measured on 86 specimens of P. wehrlei. Specimens were cleared and stained using the alizarin red method of Williams (1941). Salamanders were again placed into low elevation (26 specimens), high elevation (35) and cave groups (25) (Fig. 6). The following measurements were made with an ocular micrometer fitted on a dissecting microscope: inter-premaxillary width (IPW, least), antero-frontal width (AFW, greatest), mid-frontal width (MFW, least), otic capsule length (OCL, left side), humerus

Figure 3. Morphological (external characters) sample localities.

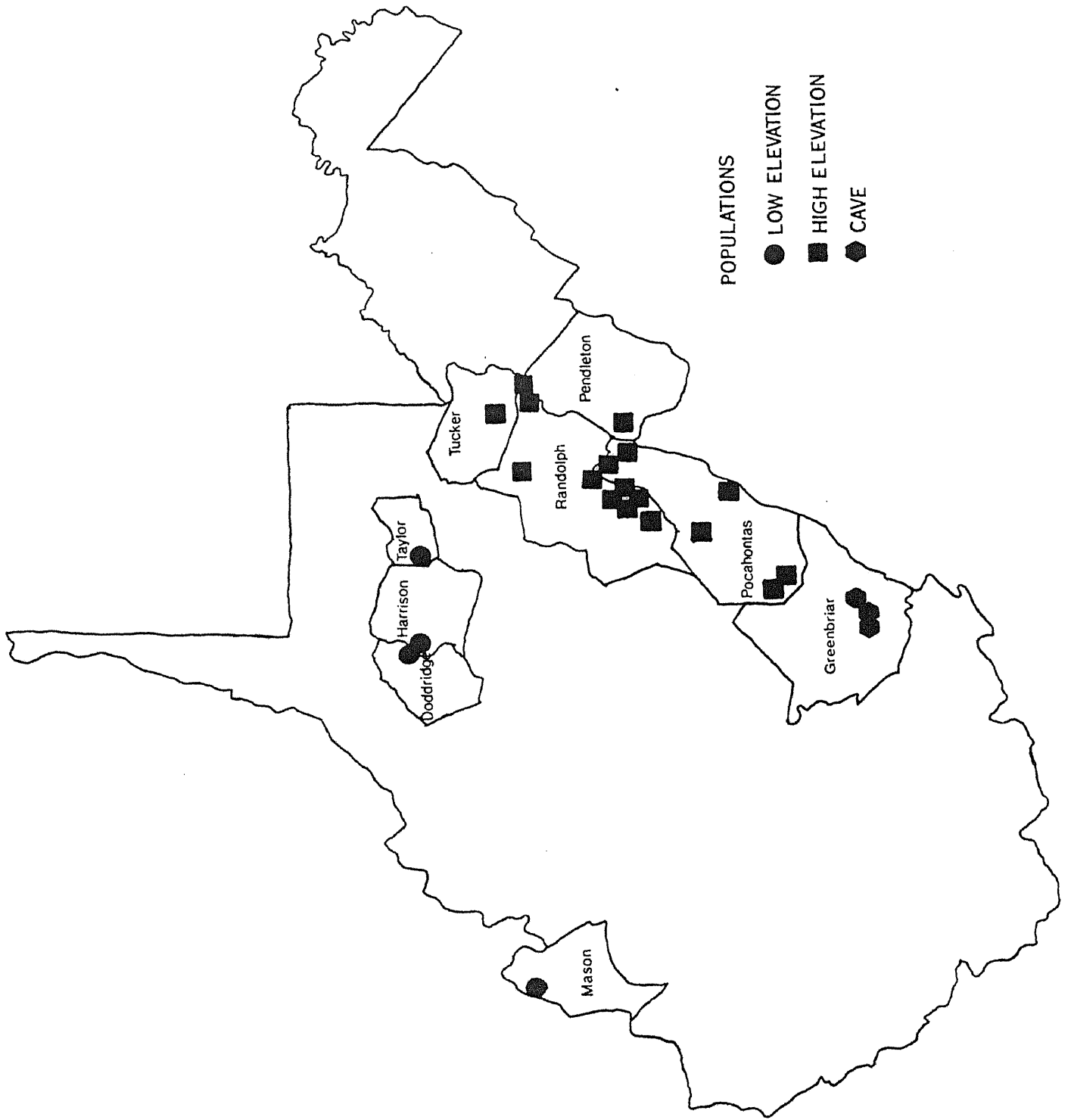


Figure 4. Measurements taken for morphological (external) characters.
Abbreviations given in text.

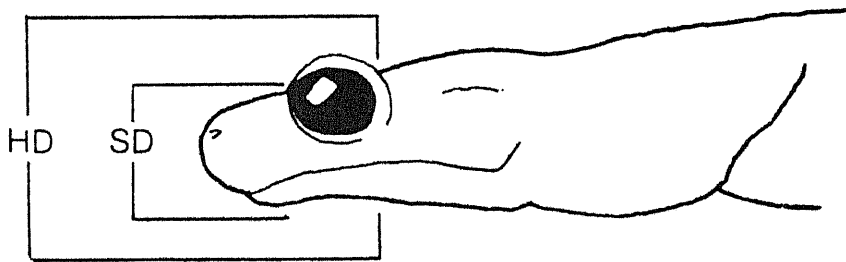
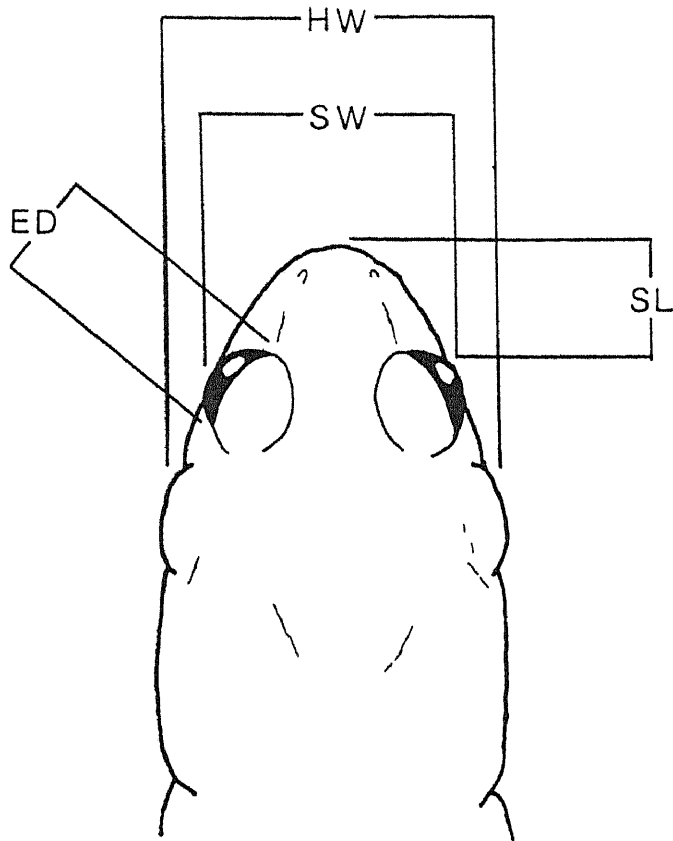


Figure 5. Measurements taken for morphological (external) analysis.
Abbreviations given in text.

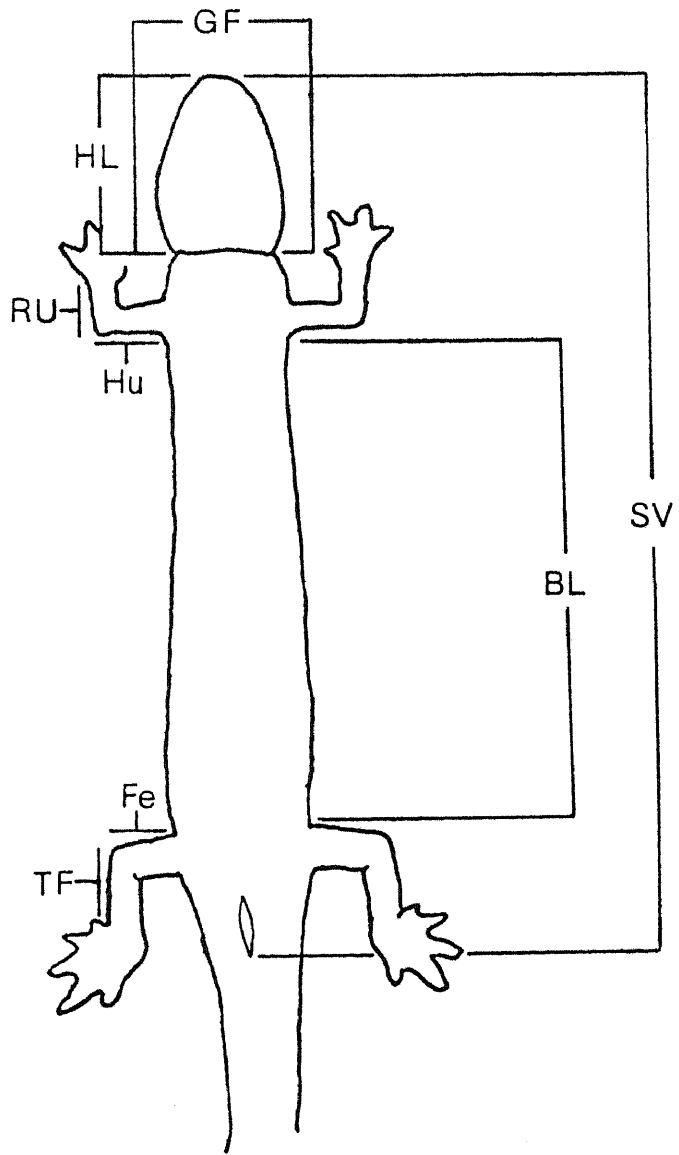
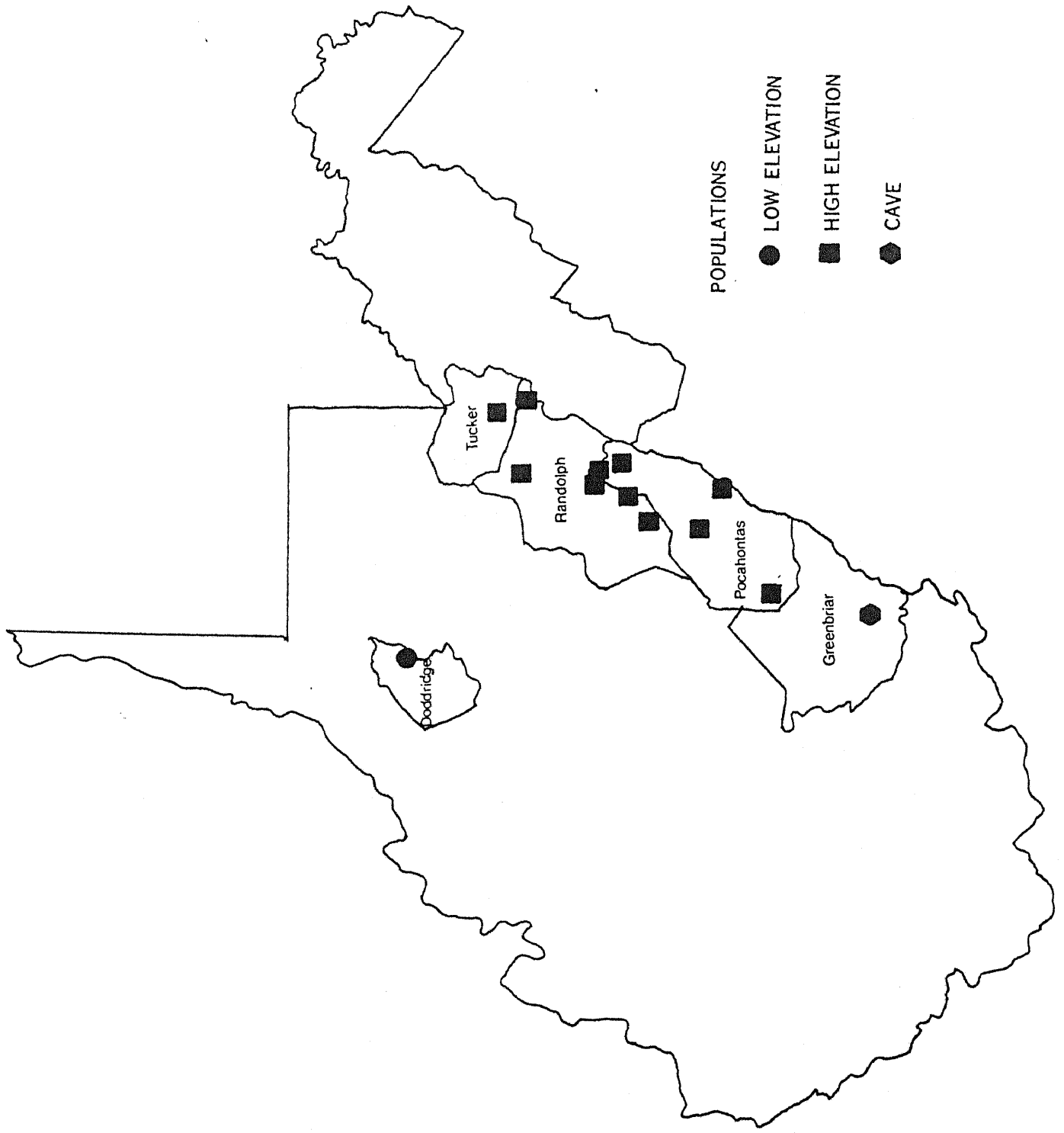


Figure 6. Morphological (skeletal characters) sample localities.



length (Hu), radius and ulna length (RU), femur length (Fe), tibia and fibula length (TF), maxillary breadth (MB, greatest), and dentary breadth (DB, greatest) (Fig. 7). Total skeletal length (TSL, from tip of snout to base of pelvic girdle) was measured to the nearest tenth of a millimeter using a Helios vernier caliper. The number of trunk vertebrae (TVN) was also recorded.

For separate morphological analyses of external and skeletal characters, regression analysis was applied to remove the effects of intraspecific size variation. The independent variable chosen for regression of all other variables was snout-vent length for external morphology and total skeletal length for skeletal morphology. "Size free" residuals for each morphological character were produced from the SAS General Linear Models procedure (Barr et al., 1976). The three populations were compared by step-wise (multivariate) discriminant analysis using the computer program BMD07M (Dixon, 1974). This treatment generates canonical variates with maximum between group variance relative to their within group variance. The canonical variate means are plotted on the first two canonical axes, and analysis of variance describes significant differences among populations. Using canonical functions, the posterior probability of each salamander belonging to its respective group is computed and classified accordingly.

Twenty-five salamanders were collected from each of the following habitats for physiological studies: low elevation, Doddridge County (374 m); cave, Greenbrier County (671 m); and high elevation, Randolph County (1067 m) (Fig. 8). Salamanders were collected on 17 May, 1981; 5 June, 1981; and 22 May, 1982, respectively. All animals were kept

Figure 7. Measurements taken for morphological (skeletal) analysis. Abbreviations given in text (After Wake, 1966).

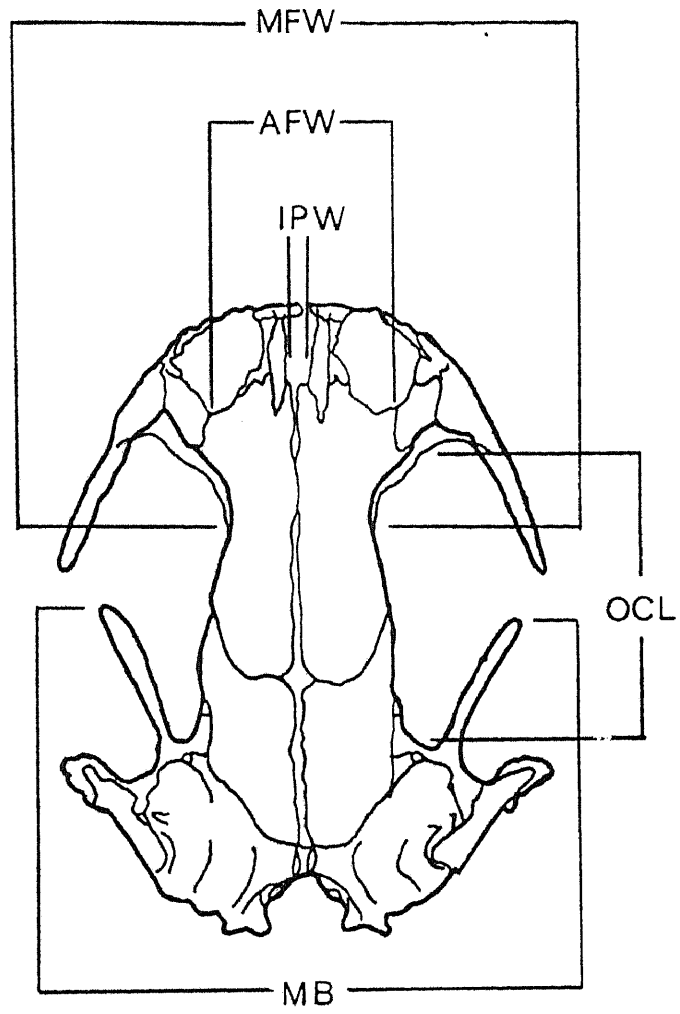
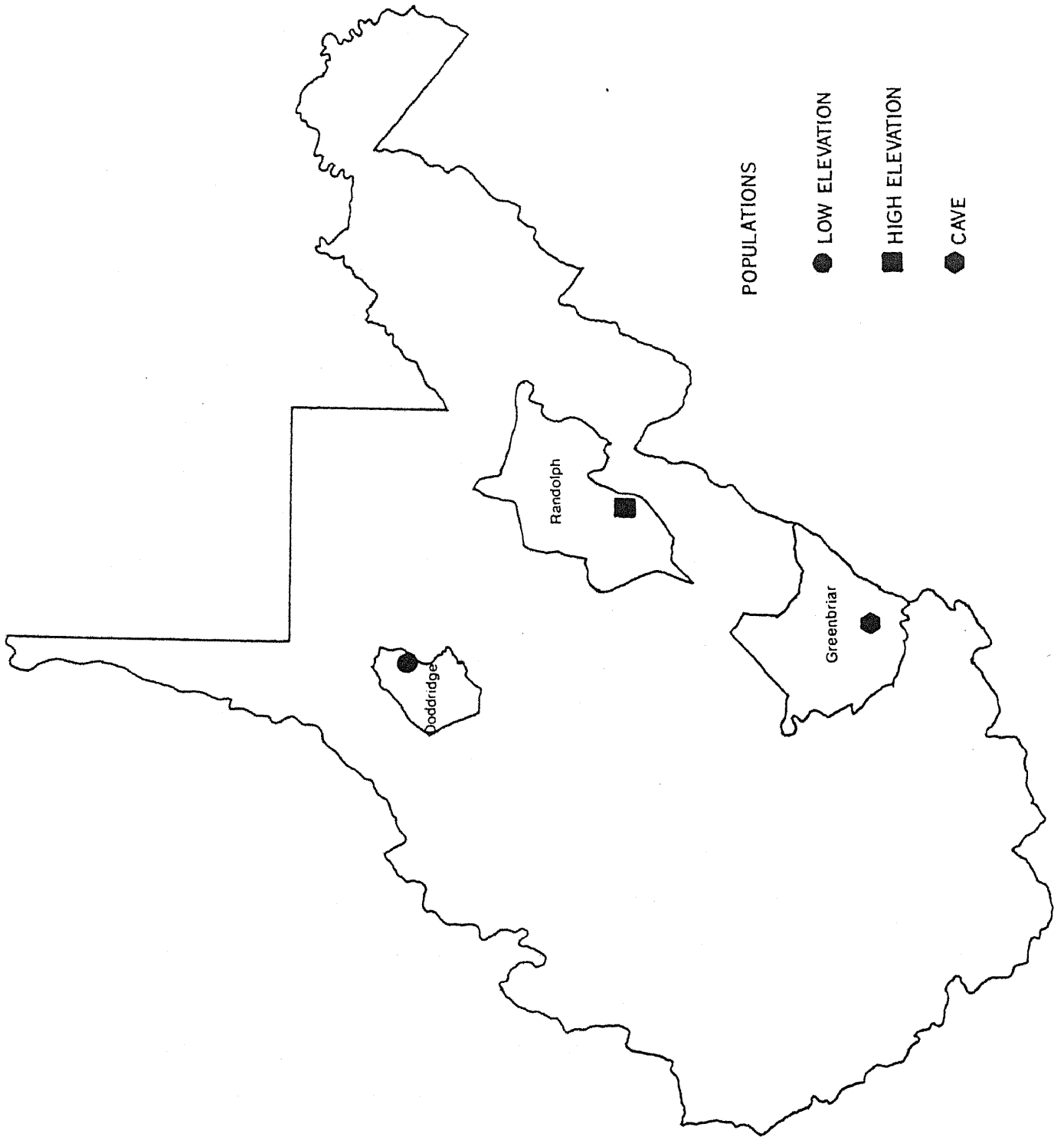


Figure 8. Sample localities for CIM and dehydration experiments.



at 20 C for six to twenty-one days before any test was performed. Critical thermal maxima (CTM) was measured by placing individuals in perforated plastic bottles and immersing them in a water bath at 20 C. Zweifel (1957) reported that CTM's of lungless salamanders do not vary when heated in air or water. A standard mercury thermometer was fitted in the lid of the bottle and temperatures were recorded to the nearest tenth of a degree. The water was heated at a rate of one to two degrees per minute. Hutchinson (1961) determined that a heating rate between one and three degrees per minute apparently eliminates deep body temperature lag. The endpoint of the CTM was determined by the loss of the righting response which occurred when the individual could not right itself after being turned over on its back (either by itself or by the experimenter). Twenty salamanders from each habitat were tested separately and t-tests were used to compare mean CTM among populations. In addition, seven cave specimens and five low elevation specimens were acclimated at 20 C for 35 to 50 days to determine the effects of long-term acclimation. Mean CTM's were compared between the two populations before and after acclimation.

Dehydration rates of P. wehrlei from the three habitats were measured by placing the salamander in a perforated plastic container of known weight. The container was lined with a plastic screen to eliminate escape routes for the smaller specimens. Test animals were blotted on paper towels to remove excess water and bladders were emptied by applying pressure to the dorsal pelvic region. The dehydration apparatus consisted of a Cenco vacuum pump which pumped air through a cylinder filled with Drierite, into a large cylinder in which the plastic container (with salamander) was placed, and then

through a flow meter. This allowed for a constant monitoring of air flow which ranged from 480 to 520 ml per minute. The plastic container plus salamander was weighed at the beginning of the experiment and at subsequent hourly intervals until cessation of throat movements. All dehydrations were carried out at the acclimation temperature (20 C). Dehydration results were expressed in several ways to determine resistance and tolerance to desiccation. For comparing resistance to dehydration (determined by the rate of weight loss per hour) among the populations, non-linear regression analysis was employed to remove the effects of size variation. Original body weight was used as an independent variable upon which hourly weight loss was regressed to produce "size free" residuals. The residuals were then used as relative values of water loss per hour. The t-test was applied to analyze possible differences among means of the three populations. Desiccation was also analyzed by two other methods. First, a t-test was used to compare mean percent total weight (= water) loss for each population, which was determined by dividing the percent weight lost by the original body weight. Then tolerance was expressed using the formula of Whitford and Hutchinson (1967) which determined the Respiratory Surface Area (RSA): $\log S = 0.983 + 0.614 \log W$, or $S = 9.62 W^{0.614}$, where S = RSA in square centimeters and W = weight in grams. This expression of water loss considered the surface of individual salamanders so as to ascertain the effects of size. Results were then expressed as weight loss (RSA) per hour in $\text{mg cm}^2 \text{ hr}$ for each population and means were compared using a t-test.

CHAPTER III

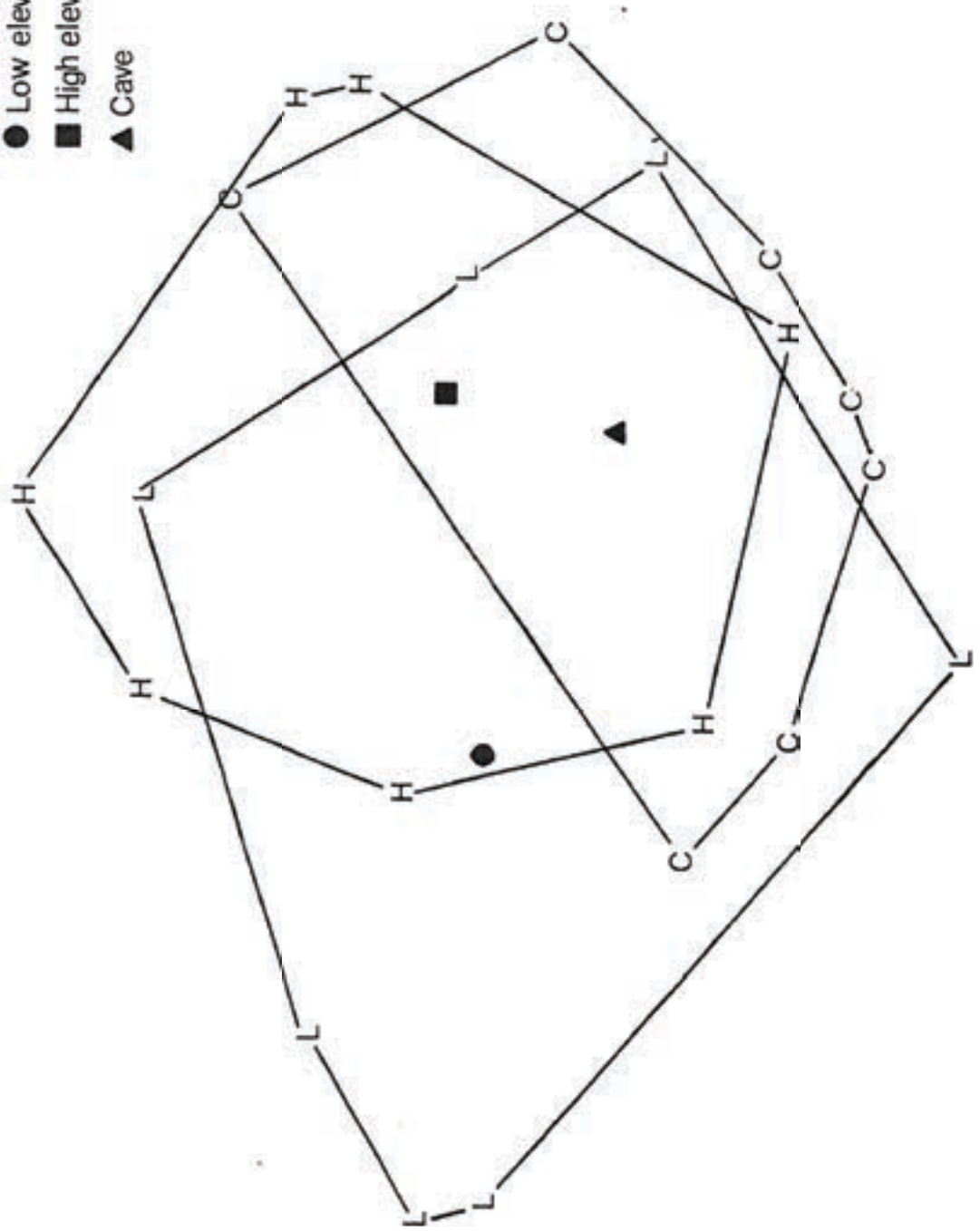
RESULTS

Discriminant analysis of external morphological characters of the three P. wehrlei populations revealed considerable overlap on the plot of the first two canonical axes (Fig. 9). A large amount of variation within each population was also observed. The first canonical axis was responsible for 77.3 percent of the total dispersion and the second axis, 23.7 percent total dispersion. Based on coefficients of canonical variables, the three most influential characters providing separation on the first axis were tibia and fibula length, snout length and head depth. On the second axis, separation was based primarily on head width, head depth and snout length. Classification of individual P. wehrlei into respective populations resulted in only 168 of the 232 (61.9%) individuals being correctly classified. Comparison of population means revealed significant difference among all three populations (F-test, $P < 0.01$).

Discriminant analysis using skeletal characters produced results similar to the external morphological analysis (Fig. 10). Extensive overlap of the three populations plotted on the first two canonical axes accompanied by substantial variation within populations was observed. The first two canonical axes accounted for 75.6 and 24.4 percent of the total dispersion, respectively. Based on coefficients of canonical variables, the most influential characters providing separation on the first axis were inter-premaxillary width, maxillary breadth, dentary breadth and tibia and fibula length. Separation on the second axis was based primarily

Figure 9. Plot of the first two canonical axes generated by discriminant analysis for external characters, representing individuals plotted most distantly from the population mean. Canonical variate means are represented by symbols, and letters represent individual skulls for cave (C), high elevation (H), and low elevation (L) groups.

- Low elevation
- High elevation
- ▲ Cave

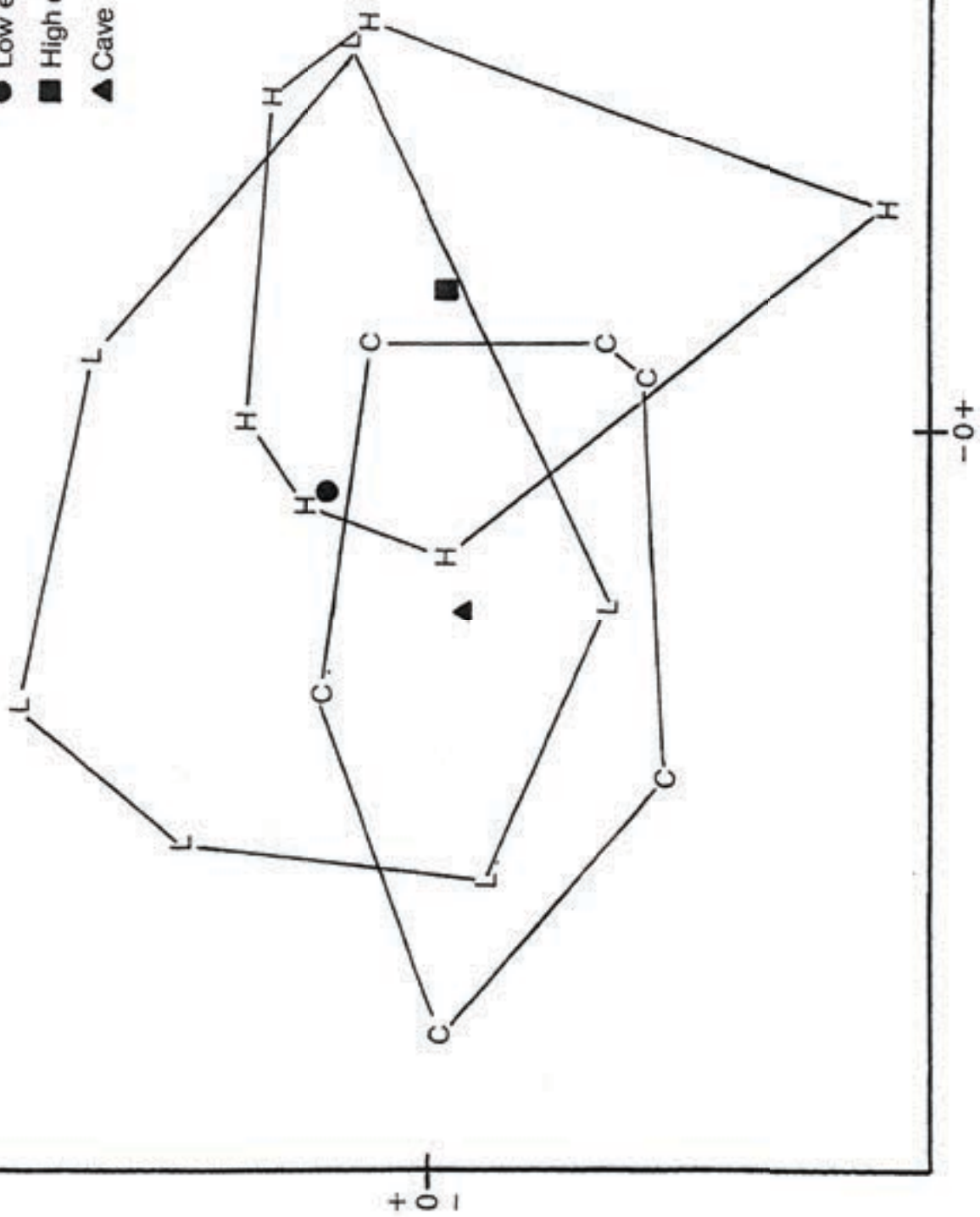


+ 0 1

- 0 +

Figure 10. Plot of the first two canonical axes generated by discriminant analysis for skeletal characters, representing individuals plotted most distantly from the population mean. Canonical variate means are represented by symbols, and letters represent individual skulls for cave (C), high elevation (H), and low elevation (L) groups.

- Low elevation
- High elevation
- ▲ Cave



on inter-premaxillary width, antero-frontal width and maxillary breadth. Classification of P. wehrlei into respective populations resulted in only 63 of the 86 (63.5%) individuals being correctly classified. Significant mean differences were found among the high elevation population to the cave and low elevation groups ($P < 0.01$). Other paired comparisons between means revealed no differences ($P > 0.01$).

Comparisons of critical thermal maxima (CTM) revealed differences among the three populations (t-test, $P < 0.05$). The cave population had the lowest mean CTM (29.90 C), the high elevation population was intermediate (30.67 C) and the low elevation population had the highest (31.89 C) (Table 1). Following long-term acclimation (35 to 50 days) of three low elevation and five cave individuals to 20 C, no significant differences in CTM were observed. This resulted from the cave population CTM rising 1.97 degrees.

Results of evaporative water loss tests are presented in Figure 11. Mean residuals, produced by regressing weight (= water) loss each hour against original body weight, were compared using a t-test and no differences ($P > 0.05$) were noted except for the first hour. The low elevation group lost significantly ($P < 0.05$) more water during the first hour of dehydration compared to the high elevation group, and the cave population was intermediate. Mean percent total water loss at death for each population was also analyzed using a t-test and no differences ($P > 0.05$) were found among populations (Table 2). The rates of dehydration per hour over the entire duration of each test are $10.34 \text{ mg cm}^2 \text{ hr}$ for the high elevation group, $11.56 \text{ mg cm}^2 \text{ hr}$ for the cave group and $12.99 \text{ mg cm}^2 \text{ hr}$ for the low elevation

Table 1. Critical thermal maxima (C) for P. wehrlei.

Group	N	$\bar{X} \pm 2(SE)$	Range
Cave	20	28.39 \pm 2(.23)	26.75-30.00
High Elevation	20	30.69 \pm 2(.19)	29.00-32.00
Low Elevation	19	31.89 \pm 2(.18)	30.50-33.50

Figure 11. Hourly relative weight loss (residuals) of P. wehrlei during dehydration experiment. Horizontal lines indicate means and rectangles indicate 2 SE above and 2 SE below the means.

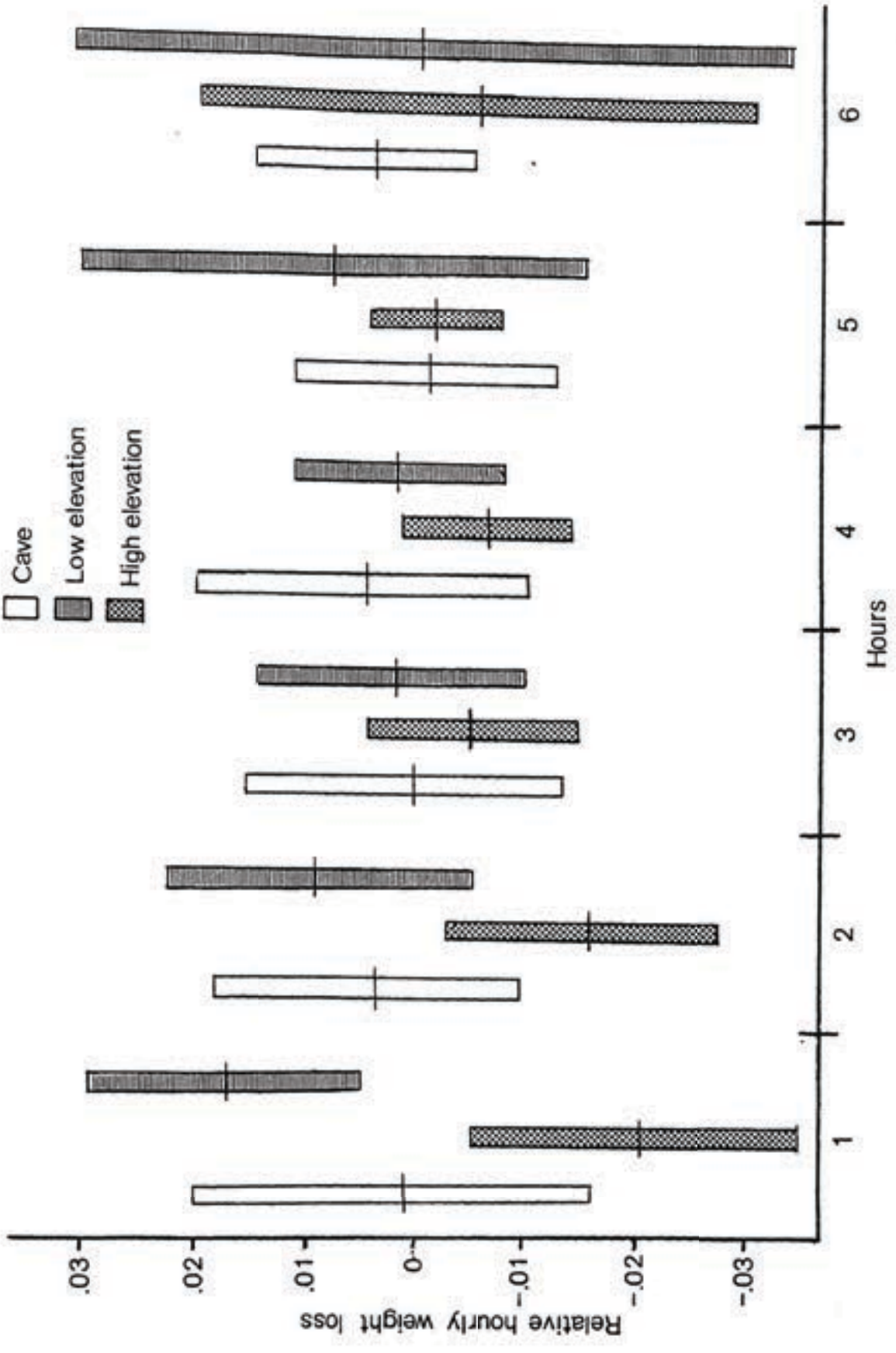


Table 2. Percent total weight (= water) loss during dehydration experiments.

Group	N	$\bar{X} \pm 2(SE)$	Range
Cave	22	41.39 \pm 2(.48)	36.39-44.01
High Elevation	20	42.22 \pm 2(1.02)	32.10-48.84
Low Elevation	21	40.07 \pm 2(.71)	35.20-45.22

group (Table 3). A t-test showed no significant difference between cave and high or low elevation salamanders. There was, however, a difference ($P < 0.05$) between the rates of dehydration for the low and high elevation groups. Rates of dehydration among the three groups did not appear to be dependent on size, as the smallest group ($\bar{X} = 1.62$ g) lost water at approximately the same rate as the largest group ($\bar{X} = 2.42$ g). Duration of survival (survival time) under dehydrating conditions also showed no relationship to size. The smallest population (by weight) (high elevation) had a mean time of 209 minutes to death, the largest population (cave) had a mean time of 215 minutes, and the intermediate size population (low elevation), a mean time of 251 minutes. The differences are significant ($P < 0.05$) comparing the low elevation to the cave groups, and low elevation to high elevation groups; but no difference ($P > 0.05$) was observed between the cave and high or low elevation groups.

Table 3. Original body weight, rates of dehydration and dehydration survival time for each group.

Group	(grams) Original Wt. $\bar{X} \pm 2(\text{SE})$	Range	(mg cm ² hr) Rate of Dehydration $\bar{X} \pm 2(\text{SE})$	Range	(min) Survival Time $\bar{X} \pm 2(\text{SE})$	Range
Cave	2.49 \pm 2(.27)	0.74-4.68	11.56 \pm 2(.55)	10.45-12.66	315 \pm 2(24.3)	290.7-339.3
High Elevation	1.69 \pm 2(.15)	0.80-3.00	10.33 \pm 2(.28)	9.78-10.20	309 \pm 2(15.9)	277.1-340.9
Low Elevation	1.83 \pm 2(.20)	0.64-4.02	12.99 \pm 2(.59)	11.82-14.16	251 \pm 2(19.5)	231.9-270.9

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Some taxonomic difficulties associated with cave dwelling P. wehrlei in southern Virginia suggested morphological divergence in cave and high elevation populations. Highton (1971) discussed two species of salamanders from southwestern Virginia, P. dixi Pope and P. jacksoni Newman, which he reduced to the synonymy of P. wehrlei. These salamanders inhabit caves and were distinguished from P. wehrlei by only minor color differences. Highton (1971) also described a new species, P. punctatus, which is closely related to P. wehrlei, but differs in color pattern and number of trunk vertebrae. This species is found only at high elevations in the Valley and Ridge Province in Virginia and West Virginia. An initial cursory observation of cave individuals from West Virginia, indicated they are much larger and heavier bodied compared to the other populations. Therefore, it was postulated that there may be some structural differences in body form (morphology) which accounts for their atypical appearance. Present results, however, show extensive population overlap on canonical plots of Plethodon wehrlei and a general morphological similarity among cave, high elevation and low elevation populations.

Differences in mean critical thermal maxima (CTM) among the three populations of P. wehrlei may be the result of differences in microhabitat. The cave population, which is found in a habitat where the temperature is relatively constant between 10 and 12 C (Davies, 1958), showed the lowest CTM. The highest CTM was found in the low elevation population which inhabits a much warmer region than

the high elevation or cave group. These results were expected, as Hutchinson (1961) has shown that salamanders can physiologically adjust their CTM when acclimated to different environmental temperatures. He also found that the CTM of the red-spotted newt, Notophthalmus viridescens, from the North Carolina Piedmont was significantly higher than those from the North Carolina mountains. Similarly, Spotila (1972) found the Plethodontid salamander, Desmognathus fuscus from an elevation of 293 m, had a significantly higher mean CTM than those found at elevations between 530-640 m. Therefore, the results of the present study support previous reports of a positive correlation between microhabitat temperature and CTM. The ecological significance of the CTM is that salamanders are able to adjust physiologically to the temperature extremes which they would normally encounter in their environment.

Thorson (1956), studying three species of anurans, reported that resistance to desiccation is not constant throughout a desiccation period of 2 to 3.5 hours. He found a brief initial reduction in the rate of water loss was followed by an extended period of rapid dehydration. He determined that this initial resistance to water loss was the result of physiological control because dead frogs exposed to the same experimental conditions did not exhibit a rate change. MacMahon (1964), however, dehydrated agar molds of salamanders and live salamanders and found no difference in their resistance to desiccation. He determined that three species of Plethodon; P. jordani, P. glutinosus and P. yonahlossee, had no physiological control over their rate of water loss and that this rate was controlled only by the salamander's morphology. The absence of morphological variation

accompanied by the general similarity in desiccation rates for the three P. wehrlei populations studied would appear to support MacMahon's (1964) conclusions. The greater water (= weight) loss during the first hour, however, when comparing low elevation to high elevation populations of P. wehrlei, suggests some variation in physiological resistance to desiccation. The greater resistance to water loss observed for the high elevation group might be explained by acclimation (adaptation) to a drier microhabitat on Cheat Mountain in Randolph County compared to the lower woodland regions of Doddridge County.

Tolerance to desiccation had been reported in salamanders as percent total weight (= water) loss (Thorson and Svihla, 1943; Littleford et al., 1947; Gordon, 1952; Thorson, 1955; Hutchinson, 1958; Ray, 1958; Larson, 1971; Pauley, 1978d) and rate of water loss (Cohen, 1952; Ray, 1958; MacMahon, 1965; Schmid, 1965; Spight, 1968; Spotila, 1972; Pauley, 1978d). Most of these studies have dealt with interspecific variation in tolerance to dehydration although a few (MacMahon, 1965; Larson, 1971) have noted intraspecific variation. MacMahon (1965) found intraspecific variation in tolerance to dehydration between low elevation and high elevation P. glutinosus. He suggested genetic control of tolerance to desiccation, because selection for greater tolerance in areas of moisture stress may have taken place. For intraspecific comparisons, the smaller the mass of an animal, the greater its relative surface area will be. Since most of the water lost in dehydration is lost through the skin (Porter, 1972), smaller animals would be expected to have a faster rate of water loss per unit of mass. Thorson (1955), Ray (1958), MacMahon (1965), Spight (1968) and Spotila (1972) have found this to be true in

salamanders whereas Littleford et al. (1947) and Cohen (1952) have not. Data from the present study on P. wehrlei do not show a relationship between size and relative rate of water loss. The high elevation group was the smallest (by weight), yet had the slowest dehydration rate while the cave group was the largest and had an intermediate rate. The low elevation group, intermediate in weight, had the fastest dehydration rate. Dehydration rates were significantly different only between the high and low elevation groups and weights were significantly different only when comparing cave to high and low elevation groups. The survival time of dehydration also shows no relationship to size. The smallest population would be expected to exhibit the shortest time to death and the largest, the longest time. However, the smallest population (high elevation) had approximately the same survival time as the largest population (cave). The relationship between survival time, size of animal and rate of dehydration may suggest a greater tolerance to dehydration in high elevation salamanders. This may again be due to acclimation or adaptation to more xeric conditions. Ray (1958) found that tolerance to water loss is directly correlated with habitat in salamanders; the drier the microhabitat the greater the tolerance to desiccation. He found this correlation for comparisons at the family, generic and occasionally at the specific level. Similarly, Larson (1971) was able to positively correlate rates of water loss to environmental moisture in three races of the salamander, Ambystoma tigrinum. Absence of differences in rates of dehydration comparing cave to low and high elevation populations may indicate that their microhabitats are less variable in moisture than first expected. The cave population,

inhabiting an area with high and constant relative humidity, was expected to be the least tolerant to desiccation. The results fail to confirm this. A possible explanation may be that these salamanders are transitory, moving freely to and from the cave and surrounding forest habitats. If this is the case, the association between rate of desiccation and habitat would suggest an elevational cline. The low elevation had the slowest rate of dehydration, the cave was intermediate, and the high elevation population had the most rapid rate of dehydration.

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APPENDIX

Appendix 1. Specimen List

Abbreviations are as follows: WVBS, West Virginia Biological Survey; TKP, private collection of Thomas K. Pauley; NBG, private collection of N. Bayard Green; RB, collection of Richard Blaney deposited into the West Virginia Biological Survey; SKG, collection of Sharon K. Gross deposited into the West Virginia Biological Survey.

Cave Group

Greenbrier County:

Arbuckle's Cave: WVBS 4060-4064, 3626-3628, 3630-3634, 3636-3639, 3641-3642, 3242-3243, 3717-3718.

McClung's Cave: WVBS 4416 (11 specimens), 3336-3339; SKG 027-051.

Cave 2.3 mi NE Lewisburg: RB 6923-6927, 6931-6934.

Higginbotham Cave: WVBS 2263, 3740.

Cave 2 mi SE Frankford: WVBS 3470.

High Elevation Group

Randolph County:

Gaudineer Knob: WVBS 1967 (2 specimens), 1283.

White Top Mountain: WVBS 3671-3676.

Barton Knob: WVBS 3719-3725, 3727, 3438, 3683-3712; NBG 482-483, 1122-1123, 1537-1538, 260-261, 1784.

Cheat Bridge: TKP 1623, 1649-1651.

Forest Rt. 92: TKP 1602-1604.

Bickle Knob: TKP 1601, 1614-1615, 1607-1608, 1657.

Mt. Porte Crayon: TKP 1658.

Cheat Mountain: SKG 051-076.

Dolly Sods: WVBS 4488.

Droop Mountain: WVBS 47.

Pochahontas County:

John's Camp Run: TKP 1652, 1654-1655.

Wildell: TKP 1636, 1634, 1627, 1628, 1635.

Burner Mountain: TKP 1644, 1648.

Briery Knob: TKP 1616.

Paddy Knob: TKP 1638-1639.

Snowshoe: TKP 1620, 1626, 1640, 1632, 1625, 1643, 1641, 1618.

Tucker County:

Mozark Mountain: WVBS 4489-4490; TKP 1629.

Pendleton County:

Big Mountain: WVBS 4491.

Low Elevation Group

Mason County: WVBS 3482-3488, 4031-4054, 3733-3734, 3736, 3738.

Taylor County: WVBS 3607-3623, 3589-3591, 3593-3605.

Harrison County: WVBS 3748, 3751-3758, 3765-3767.

Doddridge County: WVBS 388; SKG 001-026.

