

## Species Recognition for *Percina nevisense* Cope (Actinopterygii: Percidae)

**John T. Goodin**, Wetlands Division, U.S. Environmental Protection Agency, 401 M St., SW, Washington, DC 20460

**Eugene G. Maurakis**, Science Museum of Virginia, 2500 West Broad St., Richmond, VA 23220, and Biology Department, University of Richmond, Richmond, VA 23173

**Elgin S. Perry**, 2000 Kings Landing Road, Huntingtown, MD 20639

**William S. Woolcott**, Biology Department, University of Richmond, Richmond, VA 23173

### ABSTRACT

Analysis of character variation among populations of *Percina peltata* (shield darter) throughout its range indicates species-level differentiation between northern and southern populations. Populations in and south of the Chowan-Roanoke River drainage represent *Percina nevisense* (Neuse River darter). Populations in and north of the James River drainage represent *P. peltata*. These conclusions are supported by multivariate analyses of nine meristic (eight significant discriminators) and eight morphometric (seven significant discriminators) characters. Presence of cheek scales, the most prominent external discriminator in *P. nevisense*, scales above and below lateral line, scales around caudal peduncle, dorsal fin ray spines, dorsal fin pterygiophore position, and caudal peduncle depth can be used to distinguish *P. nevisense* from *P. peltata*.

### INTRODUCTION

Since first described by Stauffer (1864), *Percina peltata* (shield darter) of eastern North America has experienced an active taxonomic history. When Cope (1870) described *Percina nevisense* (Neuse River darter) he thought it so different from *peltata* that he considered assigning it to a different genus. In their description of *Percina crassa*, Jordan and Brayton (1878) referred *nevisense* to the genus *Alvordius* (with *crassa*) and did not include *P. peltata* in their summary of fish distributions. Jordan and Gilbert (1882) likewise did not include *P. peltata* in their study, but lumped *P. nevisense* with *Hadropterus maculatus* Girard as *Alvordius nevisensis*. Jordan and Evermann (1896) considered the following fishes to be *Hadropterus peltatus*: *P. nevisense*, *A. crassus*, and *A. variatus*. Jordan et al. (1930) incorporated *P. peltata*, *P. nevisense*, *H. maculatus*, and *A. crassus* as *Alvordius peltatus*. In 1948 Raney and Suttkus (unpubl.) proposed three subspecific populations for *P. peltata* (= *H. peltatus*): *P. p. peltata* (Stauffer) in drainages from the James River to the Hudson River; *P. p. nevisense* (Cope) in the Tar and Neuse rivers; and an undescribed subspecies in the upper Roanoke River system. No determination was made regarding populations in the lower Roanoke and Chowan rivers. Mayden and Page (1979) did not recognize *nevisense* as a valid taxon but noted that southern populations of *P. peltata* from the Neuse to Roanoke River drainages had partially scaled cheeks.

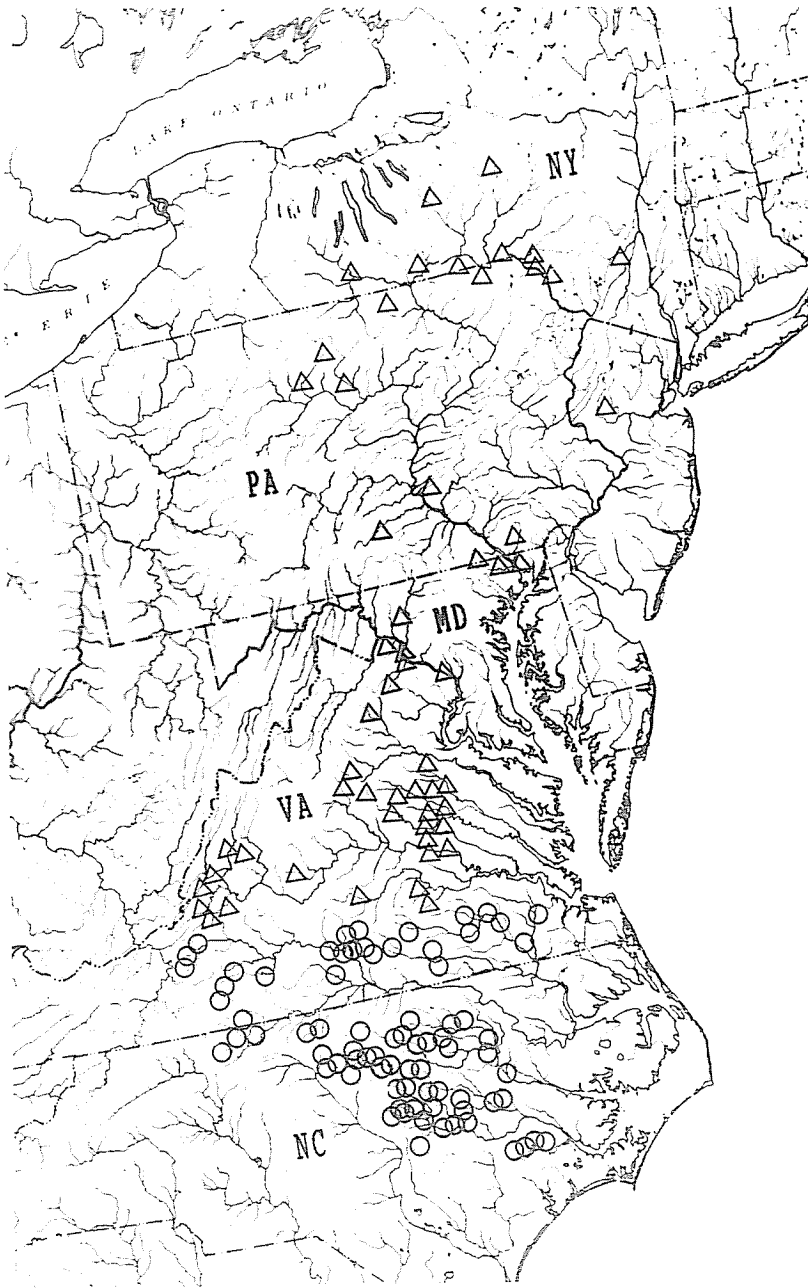


FIGURE 1. Geographical distributions of *Percina nevisense*, Roanoke-Chowan River drainage in Virginia south to Neuse River drainage in North Carolina (o), and *Percina peltata*, James River drainage in Virginia north to Hudson River drainage in New York ( $\Delta$ ).

We evaluate southern populations of *Percina peltata* (Stauffer) with a quantitative character analysis to test species recognition of *Percina nevisense* by Cope (1870).

#### METHODS

For external characters, 368 specimens of *P. peltata* were examined from 174 collections in drainages throughout its range (Fig. 1). Only specimens 25 mm SL or greater were used to reduce ontogenetic variation. Up to three specimens from each collection site were examined with two exceptions: five specimens each were examined from collections in the Potomac and Hudson River drainages where numbers of collections were limited. Although the type of *P. peltata* (*Etheostoma peltatum*, ANSP 22627) was examined, the type of *P. nevisense* (*Etheostoma nevisense*) was not. Bohlke (1984) indicated an extensive search for the type of *P. nevisense* failed to locate this fish.

Eighteen external characters were measured on each specimen following methods in Cailliet et al. (1986). Bilateral characters were evaluated on the left side. Standard length (SL), head length (HL), gape width (GW), body depth (BD), pectoral fin length (PFL), pre-dorsal length (PDL), dorsal fin base length (DFL), caudal peduncle length (CPL), and caudal peduncle depth (CPD) were measured to the nearest 0.1 mm with dial calipers. Numbers of lateral line scales (LLS), scales above lateral line (ALL), scales below lateral line (BLL), scales around caudal peduncle (CPS), dorsal fin spines (DFS), dorsal fin soft rays (DFR), pectoral fin rays (PFR), anal fin spines and rays (AFSR), and cheek scales (CS) were counted. River, drainage, latitude, and province (Montane, Piedmont, or Coastal Plain) were recorded for each specimen and used in character analyses and distributional plots.

Three internal characters were examined in 17 specimens of *P. nevisense* from five collections in the Chowan-Roanoke river drainages, and 21 specimens of *P. peltata* from three collections in the James and Rappahannock rivers. Position of first dorsal fin pterygiophore, position of first anal fin pterygiophore, and total vertebrae in each species were determined from radiographs exposed at 50 kV and 5mA for 60 sec.

Principal Components Analysis was used to assess linear structure of external character data and to explore separation among populations based on mean principal component (PC) scores as the technique assumes no *a priori* classification of specimens into species. Species groupings were established by plotting population centroids (means by population) in geometrical space spanned by the first three principal component scores. Multivariate analysis of variance (MANOVA) was used to test the null hypothesis that differences between the two species are no greater than that which might result from random variation among specimens within each species group. If this null hypothesis is rejected, characters that are the most important discriminators between species are identified using univariate analysis of variance.

Meristic and morphometric data were transformed to logarithmic metrics to improve normality and homogeneous variance properties. As scatter plots indicated that morphometric characters have a positive and near linear association with SL whereas meristic characters do not, the partial correlation matrix with effect of SL removed (shearing procedure of Bookstein et al., 1985) was used in PCA of morphometric data to remove association of morphometric characters with SL. MANOVA was modified to multivariate analysis of covariance (MANCOVA) with SL as covariate. Meristic characters were analysed using simple correlations for PCA and standard MANOVA

for confirmation of groupings. When morphometric data were analysed by stepwise discriminant analysis, SL was forced into the model and other variables were tested for their discriminating contribution beyond that of SL.

## RESULTS

For each of the meristic and morphometric data sets, there is clear separation of populations along the dimension of the first PC (Fig. 2a-b). In each figure, one group is formed by populations A-G (*P. peltata*), representing northern drainage basins (James River and north), and a second group is formed by populations H-K (*P. nevisense*), representing southern drainage basins (Chowan-Roanoke rivers and south). Second and third PC scores computed from each of the meristic and morphometric data sets did not segregate populations. The first three meristic principal components explained 54% of the variation between populations with CS, BLL, CPS and ALL loading most heavily on the first component (Table 1). The first three morphometric principal components explained 58% of the variation between populations with BD, CPD, PDL, PFL, HL and GW loading most heavily on the first component (Table 1).

MANOVA of meristic data and MANCOVA of morphometric data reject null hypotheses of equality of northern and southern populations ( $F=71.23$ ,  $p < 0.0001$ ;  $F=50.34$ ,  $p < 0.0001$ , respectively). Univariate analysis of variance shows that among meristic characters, cheek scales is by far the most significant discriminator ( $F = 272$ ,  $p < 0.01$ ; Table 2). Scales above lateral line, lateral line scales, scales below lateral line, scales around caudal peduncle, dorsal fin spines, and pectoral fin rays also contribute significantly ( $p < 0.001$ ) to differentiate *P. peltata* from *P. nevisense*. Univariate analysis of variance shows that among morphometric characters, caudal peduncle depth is the most significant discriminator ( $F > 317$ ,  $p < 0.0001$ ; Table 3) followed by body depth, pectoral fin length, gape width, pre-dorsal length, and caudal peduncle length ( $p < 0.01$ ; Table 3).

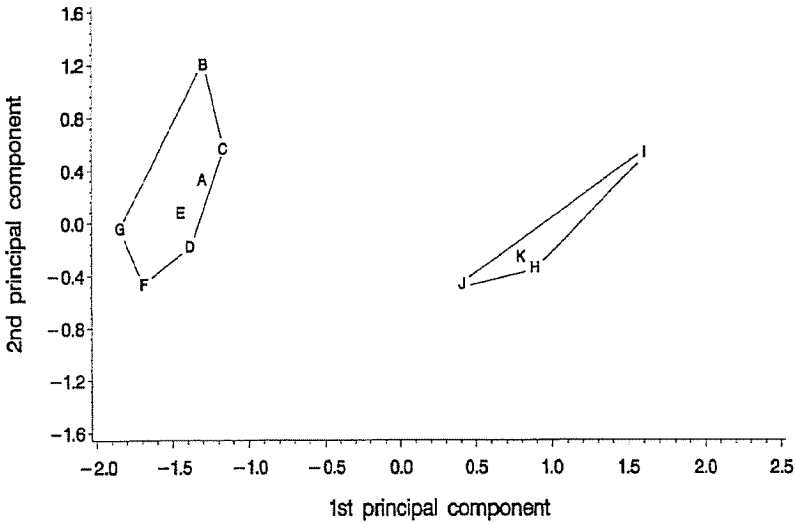
Univariate analysis of variance of individual characters confirms a pattern of differentiation in the mean score of characters between the two populations. Analysis of variance of populations representing *P. peltata* and *P. nevisense* reveals 13 of 17 characters to be significantly ( $p \leq 0.01$ ) different (Tables 2 and 3). *Percina peltata* possesses lower values in six of seven meristic characters that differ significantly. In all six significantly different morphometric characters, *P. peltata* has higher values when data are standardized to a common SL.

Frequency distributions of six significant diagnostic meristic characters (CS, LLS, ALL, BLL, DFS and CPS) reveal a break between the two populations when compared by drainage (Tables 4-9). For the most significant meristic character, number of cheek scales, values for *P. nevisense* range from 0-20 with 87.1 % possessing at least one CS; number of CS for *P. peltata* range from 0-7 with 11.1 % possessing at least one CS (Table 3). Among morphometric characters, caudal peduncle depth (narrower in *P. nevisense*) shows greatest differentiation between the species.

The first dorsal fin pterygiophore was located after the fourth vertebra in *P. nevisense* ( $\bar{x}$ , 4.06; s.d., 0.24; range, 4-5; n, 17). In *P. peltata*, the first pterygiophore occurred after the fifth vertebra ( $\bar{x}$ , 5.0; s.d., 0.31; range, 4-6; n, 21). Position of first anal fin pterygiophore in each species was located after the 20<sup>th</sup> vertebra (*P. nevisense*,  $\bar{x}$ , 20.3; s.d., 0.59; range, 19-21; n, 17; *P. peltata*,  $\bar{x}$ , 20.7; s.d., 0.5; range, 20-21; n,

2a

Meristic Characters



2b

Morphometric Characters

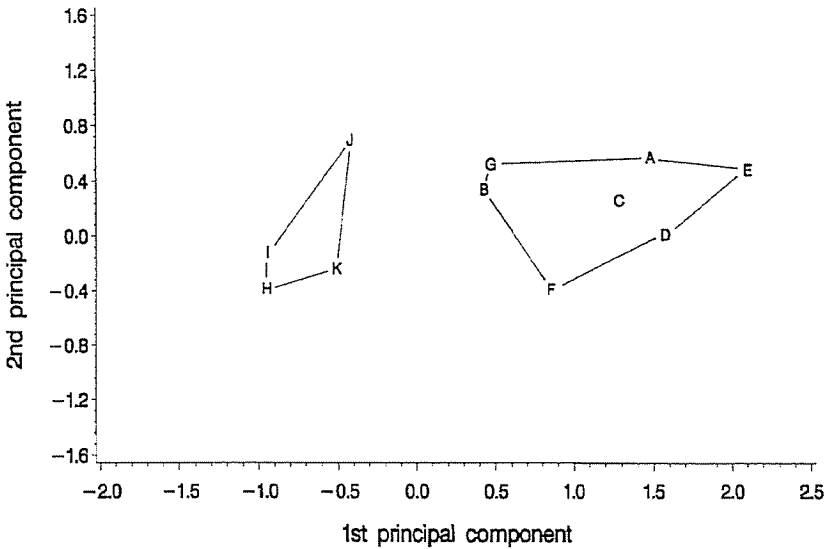


FIGURE 2a and b. River drainage distribution based on results of principal components analysis of mean values of meristic (a) and morphometric (b) characters of populations of *Percina nevisense* and *Percina peltata* (A=Hudson, B=Delaware, C=Susquehanna, D=Potomac, E=Rappahannock, F=York, G=James, H=Chowan, I=Roanoke, J=Tar, K=Neuse).

TABLE 1. Loadings of principal components (PC) analysis of meristic and morphometric characters in populations of *Percina peltata*.

Character	PC1	PC2	PC3
<b>Meristic:</b>			
lateral line scales	0.326	0.234	-0.121
scales above lateral line	0.409	-0.057	0.015
scales below lateral line	0.479	0.090	-0.270
scales around caudal peduncle	0.469	0.006	-0.282
dorsal fin spines	0.282	-0.146	0.482
dorsal fin rays	-0.026	0.621	0.394
anal fin spines and rays	-0.002	0.667	0.092
left pectoral fin rays	-0.070	0.283	-0.593
cheek scales (left side)	0.439	-0.044	0.292
proportion variance explained	0.268	0.420	0.535
<b>Morphometric:</b>			
head length	0.388	-0.222	-0.458
caudal peduncle length	0.034	-0.306	0.798
predorsal length	0.307	-0.410	-0.109
dorsal fin base length	0.045	0.737	-0.050
pectoral fin length	0.365	0.031	0.014
gape width	0.401	-0.146	-0.123
body depth	0.490	0.277	0.187
caudal peduncle depth	0.466	0.216	0.299
proportion variance explained	0.284	0.437	0.576

TABLE 2. Comparison of meristic characters between populations of *Percina nevisense* (Chowan, Roanoke, Tar and Neuse river drainages, n=224) and *Percina peltata* (Hudson, Delaware, Susquehanna, Potomac, Rappahannock, York, and James river drainages, n=144).

Character	<i>P. nevisense</i>			<i>P. peltata</i>		F	p
	$\bar{x}$	sd	(min-max)	$\bar{x}$	sd (min-max)		
Lateral line (LL) scales	59.26	3.83	(51-70)	55.74	3.64 (45-66)	121.82	0.0001
Scales above LL	7.66	0.63	(6-10)	6.79	0.78 (5-9)	145.81	0.0001
Scales below LL	10.13	1.06	(8-13)	9.06	0.94 (7-12)	83.33	0.0001
Scales around caudal peduncle	19.68	1.03	(17-22)	18.54	1.09 (16-21)	80.83	0.0001
1st dorsal fin spines	13.13	0.77	(11-15)	12.56	0.75 (10-15)	25.80	0.0001
1st dorsal fin rays	13.25	0.61	(12-15)	13.38	0.62 (12-15)	5.50	0.0195
Anal fin spines+rays	11.94	0.52	(10-13)	12.06	0.61 (10-13)	3.31	0.0696
Left pectoral fin rays	13.81	0.55	(12-15)	14.11	0.66 (12-15)	9.71	0.0020
Cheek scales (left side)	5.10	3.87	(0-20)	0.21	0.92 (0-7)	271.58	0.0001

TABLE 3. Comparison of average morphometric character values in *Percina nevisense* (Chowan, Roanoke, Tar and Neuse river drainages n=224) and *Percina peltata* (Hudson, Delaware, Susquehanna, Potomac, Rappahannock, York, and James, n=144). Morphometric characters are standardized to a common value of standard length (55.67 mm). Statistics are based on analysis of covariance for the logarithm of each character with the logarithm of standard length as covariate.

Character	$\bar{x}$	<i>P. nevisense</i>		<i>P. peltata</i>		F	p
		sd	(min-max)	$\bar{x}$	sd		
Standard length	57.04	10.59	(27.4-77.7)	53.53	8.50	(30.6-73.8)	
Head length	15.31	2.69	(8.3-20.3)	14.50	2.12	(9.2-19.5)	4.85 0.0283
Caudal peduncle length	9.07	1.93	(3.80-18.6)	8.78	1.55	(4.3-12.6)	7.54 0.0063
Predorsal length	19.46	3.63	(6.6-27.8)	18.74	2.91	(11.4-25.6)	18.99 0.0001
Dorsal fin base length	27.82	5.61	(13.7-39.6)	26.08	4.58	(14.5-36.9)	1.62 0.2044
Pectoral fin length	12.63	2.61	(6.1-19.7)	12.48	2.27	(7.4-18.5)	33.86 0.0001
Gape width	4.60	1.04	(2.1-7.7)	4.48	0.89	(2.5-7.1)	20.46 0.0001
Body depth	9.24	2.32	(3.8-15.5)	9.31	1.82	(4.9-14.1)	100.53 0.0001
Caudal peduncle depth	4.34	0.85	(2.2-6.0)	4.53	0.75	(2.7-6.3)	317.47 0.0001

TABLE 4. Frequency distribution of number of left cheek scales in *Percina nevisense* and *Percina peltata*.

	No. of Cheek Scales																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>P. nevisense</i>																					
Chowan	5	3	3	5	5	3	7	2	4	3	1	0	2	1	0	0	0	0	0	0	0
Roanoke	13	1	3	4	7	7	4	3	2	1	1	1	1	1	0	1	0	0	0	0	0
Tar	5	2	5	3	4	3	4	1	1	1	3	1	1	1	0	1	0	0	0	0	0
Neuse	14	5	5	6	4	14	8	13	9	10	3	4	4	3	0	1	0	0	1	0	1
Total	37	11	16	18	20	22	23	19	16	15	8	6	8	6	0	3	0	0	1	0	1
<i>P. peltata</i>																					
Hudson	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Delaware	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Susquehanna	38	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potomac	11	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rappahannock	12	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
York	25	3	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
James	23	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	132	7	0	4	5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0

21). Total vertebrae averaged 42.9 (s.d., 0.83; range, 42-45; n, 17) in *P. nevisense*, and 42.95 (s.d., 0.80; range, 41-44; n, 21) in *P. peltata*.

DISCUSSION

*Percina nevisense* is morphologically distinct from *P. peltata* and merits specific recognition. Cope (1870) noted *P. nevisense* had scaly cheeks and a lesser ratio of HL to SL compared to *P. peltata*. Our analyses confirm the importance of cheek scales in distinguishing the two species. In combination with cheek scales, six other meristic characters (lateral line scales, scales above and below lateral line, scales around caudal peduncle, dorsal fin spines, and position of first dorsal fin pterygiophore) can be used to diagnose *P. nevisense* and *P. peltata* (Table 10). Our significant LLS, ALL, BLL,

TABLE 5. Frequency distribution of lateral line scales in *Percina nevisense* and *Percina peltata*.

	Lateral Line Scale															
	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>P. nevisense</i>																
Chowan	1	0	0	1	1	2	4	1	3	3	4	1	2	5	4	9
Roanoke	1	0	0	1	1	2	4	1	3	3	4	1	2	2	2	1
Tar	1	0	0	1	1	2	4	2	2	3	6	2	2	2	4	2
Neuse	1	0	0	1	1	2	1	1	4	8	9	12	17	13	17	6
Total	4	0	0	4	4	8	13	5	12	17	23	16	23	22	27	18
<i>P. peltata</i>																
Hudson	0	0	0	0	0	0	0	0	0	1	0	0	2	1	1	1
Delaware	0	0	0	0	0	0	0	1	2	1	2	2	3	2	1	1
Susquehanna	0	0	0	0	0	0	1	2	3	3	1	2	6	5	6	2
Potomac	0	0	0	0	0	0	1	2	3	2	2	1	1	1	1	1
Rappahannock	1	0	0	1	0	0	2	1	4	1	1	2	1	1	1	1
York	1	0	0	1	1	2	2	5	2	4	2	4	5	1	1	1
James	1	0	0	1	1	2	4	3	3	3	1	3	2	2	1	1
Total	3	0	0	3	2	4	10	14	17	15	9	14	20	13	12	8

TABLE 6. Frequency distribution of scales above lateral line in *Percina nevisense* and *Percina peltata*.

	Scales Above Lateral Line					
	5	6	7	8	9	10
<i>P. nevisense</i>						
Chowan	2	1	23	19	1	0
Roanoke	2	2	14	30	2	0
Tar	2	2	9	13	5	0
Neuse	2	2	39	60	5	1
Total	8	7	85	122	13	1
<i>P. peltata</i>						
Hudson	0	5	1	0	0	0
Delaware	1	10	3	2	1	0
Susquehanna	1	6	21	11	1	0
Potomac	1	3	8	1	1	0
Rappahannock	1	2	10	1	1	0
York	2	4	22	1	1	0
James	2	9	12	3	1	0
Total	8	39	77	19	6	0

and CPS values that discriminate *P. nevisense* from *P. peltata* are comparable to those reported by Mayden and Page (1979) for various populations of *P. peltata* they examined throughout its formerly recognized range. Even though *P. nevisense* and *P. peltata* occur in different drainages and can be separated by meristic features, body form (relation of body depth and caudal peduncle depth) can also be used in the field to distinguish the two species. These two morphological characters demonstrate that *P. nevisense* has a slimmer profile than that of *P. peltata*. The caudal peduncle of *P. nevisense* appears pinched due to the sharper dorsal slope, particularly the ventral slope from the maximum body depth to the narrower caudal peduncle depth.



TABLE 7. Frequency distribution of scales below lateral line in *Percina nevisense* and *Percina peltata*.

	Scales Below Lateral Line						
	7	8	9	10	11	12	13
<i>P. nevisense</i>							
Chowan	2	4	9	18	13	1	0
Roanoke	2	4	4	8	22	13	1
Tar	2	1	9	11	4	2	1
Neuse	2	5	34	40	20	5	1
Total	8	14	56	77	59	21	3
<i>P. peltata</i>							
Hudson	0	1	4	0	1	0	0
Delaware	1	1	10	5	1	0	0
Susquehanna	1	11	15	11	2	0	0
Potomac	1	4	6	2	1	0	0
Rappahannock	1	3	5	5	1	0	0
York	2	9	9	8	1	0	0
James	2	6	11	5	1	1	0
Total	8	35	60	36	8	1	0

TABLE 8. Frequency distribution of scales around caudal peduncle of *Percina nevisense* and *Percina peltata*.

	Scales Around Caudal Peduncle						
	16	17	18	19	20	21	22
<i>P. nevisense</i>							
Chowan	1	4	6	8	18	8	4
Roanoke	1	4	1	5	23	13	6
Tar	1	1	5	8	12	1	6
Neuse	1	1	17	36	44	7	6
Total	4	10	29	57	97	29	22
<i>P. peltata</i>							
Hudson	0	0	2	2	2	0	0
Delaware	0	1	5	5	5	1	0
Susquehanna	1	7	17	5	8	1	0
Potomac	1	3	7	2	1	1	0
Rappahannock	1	3	4	3	5	1	0
York	1	2	14	6	7	1	0
James	1	4	13	3	5	1	0
Total	5	20	62	26	33	6	0

Position of first dorsal fin pterygiophore also discriminates between the two species. In *P. nevisense* the first dorsal fin pterygiophore is between the fourth and fifth vertebrae; that in *P. peltata* is between the fifth and sixth vertebrae. Pterygiophore position is reflected in the proportionally shorter PDL in *P. nevisense*. These results are corroborated by those of Orrell et al. (1998), who used cleared and double-stained specimens of each species in a phylogenetic study of relationships among *Percina* (*Alvordius*) species (*P. nevisense*, pterygiophore between fourth and fifth vertebrae, n=3; *P. peltata*, pterygiophore between fifth and sixth vertebrae, n=8).

Principal components analysis demonstrates species level differentiation between the Chowan-Roanoke drainage and James River drainage populations (Fig. 2a-b).

TABLE 9. Frequency distribution of dorsal fin spines in *Percina nevisense* and *Percina peltata*.

	Dorsal Fin Spines					
	10	11	12	13	14	15
<i>P. nevisense</i>						
Chowan	1	1	4	25	14	1
Roanoke	1	2	23	18	3	2
Tar	1	2	2	18	6	1
Neuse	1	2	9	56	36	4
Total	4	7	38	117	59	8
<i>P. peltata</i>						
Hudson	0	1	0	4	1	0
Delaware	0	1	6	9	2	0
Susquehanna	1	1	16	15	6	0
Potomac	1	1	6	5	1	1
Rappahannock	1	1	5	9	1	1
York	1	1	18	9	1	1
James	1	2	13	10	1	1
Total	5	8	64	61	13	4

TABLE 10. Diagnostic meristic characters of *Percina nevisense* and *Percina peltata*.

Character	<i>P. nevisense</i>		<i>P. peltata</i>	
	mode	$\bar{x}$	mode	$\bar{x}$
Cheek scales	6	4.6	1	0.2
Lateral line scales	59	59.3	57	55.7
Scales above lateral line	8	7.7	7	6.7
Scales below lateral line	10	10.2	9	9.1
Scales around caudal peduncle	20	19.7	18	18.6
Dorsal fin spines	13	13.1	12	12.6
1st dorsal pterygiophore origin	4-5th vertebra		5-6th vertebra	

Assuming no *a priori* groupings, mean PC scores for populations in the Chowan-Roanoke drainage and drainages south segregate clearly from those in the James River and drainages north using either meristic or morphometric characters.

Hybridization of *P. peltata* with the heavily cheek-scaled *P. notogramma* may account for some cheek-scaled *P. peltata*. All cheek-scaled *P. peltata* occur in drainages where *P. notogramma* is now present, except for a small percentage of fish in the Susquehanna drainage. *Percina notogramma* × *P. peltata* hybrids have been documented in James and York drainages (Loos and Woolcott, 1969) where the percentage of cheek-scaled *P. peltata* is highest in our study.

Among populations of *P. nevisense* throughout its range, variations occur in some meristic and morphometric characters (e.g. lower counts of DFR in Coastal Plain Tar; greater PFL in Coastal Plain Tar and Neuse; higher counts of LLS and BLL in Montane and Piedmont Roanoke; and higher counts of CPS in Piedmont and Coastal Plain Chowan, and Montane and Piedmont Roanoke) that may reflect effects of physiography and/or isolation of inter-drainage populations of the species. However, no effort

was made to analyze variations within drainages, nor to evaluate subspecific designations like that proposed by Raney and Suttkus (1948) for the population of *P. nevisense* in the upper Roanoke River drainage.

#### MATERIALS EXAMINED

Materials are listed by river drainage, institution, catalog number or collection number of collector (H, Haxo; REJ, R. E. Jenkins; LOM, L. O. Mohn; MDN, M. D. Norman; P, Petrimoulx; JRR, J. R. Reed; S, Southwick; and TZ, T. Zorach), and number of specimens examined in parentheses. Institutional abbreviations follow Leviton et al. (1985).

*Percina peltata*. Hudson: AMNH 41830(1), 45619(5); Delaware: CU 26996(3), 35535(2), 49694(2), 65937(3), 69042(3), 69134(3), USNM 116624(1); Susquehanna: CU 16507(3), 21628(1), 22370(3), 23337(3), 26961(3), 27049(2), 27070 (2), 34181(1), 41829(1), 42928(3), 49501(2), 53658(1), 69579(3), 69608(2), 69615(3); USNM 244275(1), 244279(2); NCSM 4620(3); Potomac: ANSP 81179(1), 81205(1); CU 13060(1), 26067(3), 31514(2); USNM 131758(5); Rappahannock: CU 9908(3), 11950(1), 2229(3), 2270(3), 2430(1), 3042(3); York: CU 51942(3), RC JRR-B138(3), JRR-B2000(3), UR 1319(2), 2240(3), 2784(3), 3187(1), 3337(2), 4379(3), 4463(3), 4601(3); James: CU 25449(3), RC LOM(1), LOM18July1973(1), LOM18July1973(3), LOM20July1973(1), LOM23July1973(1), LOM25July1973(3), REJ391(1), REJ499(1), REJ891(3), REJ1024(3), REJ1026(3), UR 366(1), 4149(1). Radiographs: James. UR3465 (13), UR4795 (4). Rappahannock. UR3078 (4).

*Percina nevisense*. Chowan: RC H153(3), H161(1), MDN87(2), MDN88(3), MDN91(3), MDN106(3), MDN/S/VCGIF(3), P33(1), REJ821(3), REJ822(3), REJ823(1), REJ908(3), REJ909(3), REJ910(2), REJ911(1), REJ1032(3), TZ165(3), TZ170(3); Roanoke: CU 10890(1), 18637(2), 18638(3), 24767(1), 42688(1), 42689(1), 50389(3); NCSM 2853(2), 3231(3), 4302(1), 7103(2), 7128(1); RC DLJ4P(3), REJ342/344(3), REJ 402(3), REJ433(2), REJ738(1), REJ912(1), REJ922(1), REJ963(2), REJ1001(3), REJ1002(1), REJ1010(1), REJ1034(3), REJ1116(3); Tar: CU 9367(2); NCSM 3084(3), 3101(3), 3120(2), 8396(1), 9289(1), 9328(1), 9635(1), 9726(1), 9766(2), 10145(3), 10158(2), 12789(1), 12814(2), 12828(1), 12879(1); Neuse: CU 10581(2); NCSM 474(3), 519(3), 548(2), 631(2), 639(1), 715(3), 755(2), 846(3), 1524(2), 1799(2), 1896(2), 1922(3), 1979(3), 2218(2), 2336(1), 3140(1), 3426(3), 3650(3), 3741(1), 3772(1), 3862(3), 4085(1), 4907(1), 5339(1), 5348(3), 5434(3), 5629(3), 6339(3), 7791(1), 8043(2), 8098(1), 8153(2), 8195(1), 8216(3), 8232(3), 8253(3), 8271(1), 8301(1), 8441(1), 8688(2), 8697(1), 10527(2), 10547(2), 10559(1), 12381(3), 12424(3), 12435(1), 12711(3), 12986(3), 13000(2). Radiographs: Chowan-Roanoke. UR3966 (3), UR4116 (4), UR 4807 (3), UR4813 (3), UR4828 (4).

#### ACKNOWLEDGMENTS

This paper is dedicated to Bill Woolcott, longtime friend and colleague, who died 18 April 1998. Gratitude is expressed to the following: J. J. Loos for assistance with initial computer programs; R. E. Jenkins for initial consultation on the study; B. B. Collette, R. E. Jenkins and L. M. Page for reviews of manuscript drafts with suggestions for its improvement; F. Schwartz for assistance with radiographs; and N. H. Wooding for assistance with preparation of the distributional map. Financial assistance was

provided by grants from University of Richmond Undergraduate Research Fund and the Robert F. Smart Student Summer Research Award. Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Cornell University, North Carolina State Museum, Roanoke College, United States National Museum provided specimens.

## LITERATURE CITED

- Bohlke, E. B. 1984. Catalog of the type specimens in the ichthyological collection of the Academy of Natural Sciences of Philadelphia. Sp. Publ. 14. Acad. Nat. Sci. Phila.
- Bookstein, F. L., B. Chernoff, R. L. Elder, J. m. Humphries, Jr., G. R. Smith, and R. E. Strauss. 1985. Morphometrics in Evolutionary Biology. Spec. Publ. 15. Acad. Nat. Sci. Philadelphia. 277 p.
- Cailliet, G. M., M. S. Love, and A. W. Ebeling. 1986. Fishes: A Laboratory Manual on Their Structure, Identification, and Natural History. Wadsworth Publishing Co., Belmont, CA. 194 p.
- Cope, E. D. 1870. On some etheostomine perch from Tennessee and North Carolina. Proc. Amer. Phil. Soc. 11:261-270.
- Jordan, D. S., and A. W. Brayton. 1878. *Alvordius crassus*, sp. nov. Bull. U.S. Natl. Mus. 12:12,82.
- \_\_\_\_\_, and B. W. Evermann. 1896. The Fishes of North and Middle America. Bull. U.S. Natl. Mus. 47:1034.
- \_\_\_\_\_, \_\_\_\_\_ and H. W. Clark. 1930. Etheostomidae. p. 282-284. Check list of the fishes of North and Middle America. U.S. Government Printing Office, Washington.
- \_\_\_\_\_, and C. H. Gilbert. 1882. *Alvordius* Girard. Bull. U.S. Natl. Mus. 16:500-505.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I, Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802-832.
- Loos, J. J., and W. S. Woolcott. 1969. Hybridization and behavior in two species of *Percina* (Percidae). Copeia 1969(2):374-385.
- Mayden, R. L. and L. M. Page. 1979. Systematics of *Percina roanoka* and *P. crassa*, with comparisons to *P. peltata* and *P. notogramma* (Pisces: Percidae). Copeia 1979(3):413-426.
- Orrell, T. M., W. S. Woolcott, and E. G. Maurakis. 1998. Phylogenetic relationships of *Percina* (*Alvordius*). In review.
- Raney, E. C. and R. D. Suttkus. 1948. The subspecies of the shielded darter, *Hadroterus peltatus*. Unpubl. abstract. 28th Ann. Meeting Amer. Soc. Ich. and Herp. New Orleans:2.
- Stauffer, J. 1864. *Etheostoma peltatum*. Proc. Acad. Nat. Sci. Phila. 1864:232-233.