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Hybridization in Umbridae in the Hudson River, New York, with Designation of Neotypes for *Umbra limi* and *Umbra pygmaea*

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Abstract

We document the occurrence of a natural hybrid between the Eastern Mudminnow, *Umbra pygmaea* (DeKay 1842) and the Central Mudminnow, *U. limi* (Kirtland 1840). Hybrid individuals were collected in a supratidal pool in a fresh-tidal marsh in the Hudson River, New York. ANOVA, ANCOVA, principal components analysis, and discriminant function analysis of meristics and morphometrics showed that the hybrids were distinguishable from the parental species and were generally intermediate between them. The tidal Hudson River is the only place these species are sympatric, and hybridization must have occurred within the last several decades. We designate neotypes for *Umbra pygmaea* and *Umbra limi.*

Key words: Central Mudminnow, Champlain Canal, Eastern Mudminnow, Erie Canal, fish dispersal, James DeKay, Jared Kirtland, type locality, zoogeography

Introduction

There are two species of Umbridae in the Eastern United States (Lee et al. 1980 *et seq.*): the Central Mudminnow (*Umbra limi*) and the Eastern Mudminnow (*U. pygmaea*). Phylogenetic analyses indicate that these two species are sister taxa (Cavender 1969, Kettler et al. 1986, López et al. 2000, López et al. 2004, Nelson 1972, Wilson and Veilleux 1982). Recently, we received a mudminnow collection from Manitou Marsh, a fresh to brackish tidal marsh in Putnam County, New York (Fig. 1). A subsequent collection (1998) of mudminnow from a supratidal pool in Manitou Marsh contained individuals that were not easily classified as either species. Geographic distinctions are no longer possible in the Hudson River Valley, and the specimens collected in Manitou Marsh (New York State Museum—NYSM 55623) had color patterns not readily classified as either striped or blotched. Smith (1985) provided a table of meristics and morphometrics for both

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mudminnows and, although he only examined five specimens of each species, identified several differences between them. The purposes of this paper are to present evidence of hybridization between these two species of mudminnow in nature and to designate neotypes for *Umbra limi* and *Umbra pygmaea*.

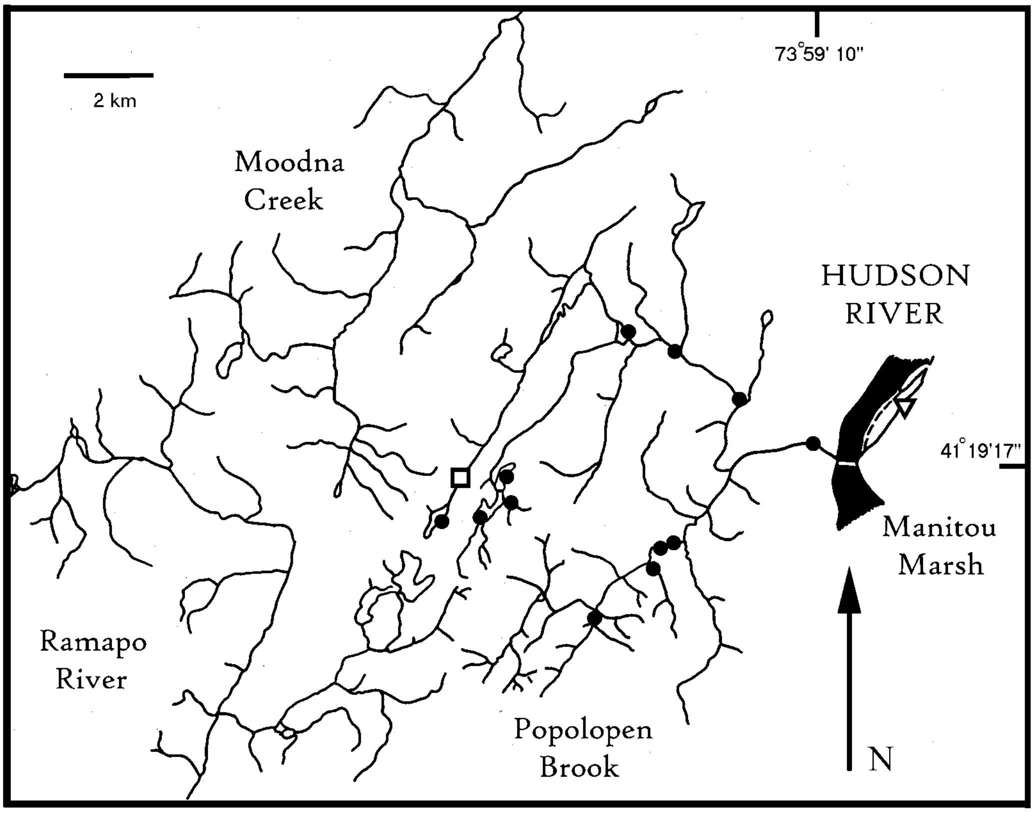

FIGURE 1. Popolopen Brook watershed in relation to Manitou Marsh and contiguous drainages. Circles are sites sampled in the 1936 survey (Greeley 1937), the square indicates collection sites for *Umbra pygmaea* in the 1990s, and a triangle (right side of map) in Manitou Marsh indicates the collection site (1998) for the hybrids.

Umbra pygmaea is native to the Hudson River drainage, New York, and the type locality is the Sparkill, a Hudson River tributary (DeKay 1842). Lee et al. (1980 *et seq.*) showed that the ranges of *U. pygmaea* and *U. limi* did not overlap in New York State and that *U. limi* was absent from the Hudson River drainage but was present to the north in the Lake Champlain watershed and to the west in the Oswego River watershed. Smith (1985) documented *U. limi* from the tidal Hudson River and its major tributary, the Mohawk River. We have specimens of *U. limi* from the Hudson River in 1976 (NYSM 1310, 11672). *Umbra limi* may have extended its range into the Hudson River from the north through the Champlain Canal or from the west through the Erie Canal sometime since the 1890s when the number of locks was reduced, the locks were enlarged, and the river channel was used for ship traffic (Daniels 2001). Alternatively, they may have been directly introduced into the Hudson watershed.

Although isolated specimens of *U. limi* have been collected from the tidal Hudson River well south of the northern extent of the salt front, their preferred habitat appears to be in supratidal pools in fresh tidal marshes, a habitat that is rare and rarely sampled. Erik Kiviat (Hudsonia Ltd., *pers. comm.*) collected specimens in 1973 from a Hudson River supratidal pool. Beebe and Savidge (1988) listed both *Umbra* species from the tidal Hudson River but examination of four of their specimens (NYSM 14350, 14367, 14490) indicated that *U. pygmaea* was probably misidentified. Thus far, no verified records of *U. pygmaea* exist for the tidal Hudson River, and the species is limited to tributaries west of the estuary: Wallkill River, Moodna Creek, and Sparkill Creek (Smith 1985).

All authors of regional or national identification manuals who were required to distinguish between *U. pygmaea* and *U. limi,* did so by geography or color pattern (Cooper 1983, Eddy 1969, Moore 1968, Page and Burr 1991, Smith 1985, Werner 2004). *Umbra pygmaea* is usually described as striped whereas *U. limi* has vertical bars or blotches.

Methods

We measured standard length, predorsal length, length of anal base, head length, snout length, eye diameter, and interorbital distance with a digital caliper. We also counted dorsal and anal fin rays and lateral line scales. All specimens examined are at the New York State Museum. We did not examine individuals smaller than 30 mm SL. *Umbra limi* specimens were from the tidal Hudson River and the Black River and Lake Champlain watersheds of the St. Lawrence drainage. *Umbra pygmaea* specimens were from southeastern New York, including the type locality, and from Long Island, New York.

Specimens examined: *Umbra pygmaea*: NYSM 1435—Sparkill at Tappan, Rockland Co., NY, August 8, 1936, 20 specimens (48.8–69.9 mm SL); NYSM 17656—Tributary to Beaver Lake, Suffolk Co., NY, August 30, 1985, 14 specimens (38.0–52.9 mm SL); NYSM 43227—Spruce Lake, Orange Co., NY, August 16, 1936, 3 specimens (35.6–55.4 mm SL); NYSM 46685—Little Cedar Pond, Orange Co., NY, July 27, 1996, 1 specimen (70.3 mm SL); NYSM 48330—Eagle Lake, Orange Co., NY, August 5, 1998, 2 specimens (30.9–50.0 mm SL); NYSM 48360—McKeays Meadow off county Rt. 48, Orange Co., NY, August 5, 1998, 3 specimens (32.0–52.5 mm SL); NYSM 48764—Patchogue River, Suffolk Co., NY, August 26, 1998, 4 specimens (30.1–58.2 mm SL).

Umbra limi: NYSM 38—Hudson River at River Mile 36, Westchester Co., April 2, 1980, 1 specimen (41.0 mm SL); NYSM 1310—Hudson River at Verplanck, Westchester Co., NY, April 14, 1976, 1 specimen (46.4 mm SL); NYSM 6905—Bowline Pond, Rockland Co., Hudson River, NY, March 31, 1979, 1 specimen (54.6 mm SL); NYSM

7688—Roseton power plant intake, Orange Co., Hudson River, NY, March 28, 1978, 1 specimen (65.5 mm SL); NYSM 11672—Hudson River at River Mile 127, Columbia Co., April 6, 1976, 1 specimen (57.8 mm SL); NYSM 24922—Pine Brook Reservoir, Washington Co., NY, July 23, 1986, 15 specimens (48.7–83.6 mm SL); NYSM 36584—Coxsackie Cove, Greene Co., Hudson River, NY, March 7, 1991, 1 specimen (44.1 mm SL); NYSM 36585—Hudson River north of Coxsackie Cove, Greene Co., March 7, 1991, 1 specimen (43.8 mm SL); NYSM 48277—Moss Lake outlet, Herkimer Co., July 28, 1998, NY, 23 specimens (48.6–76.1 mm SL); NYSM 48286—Dart Lake inlet, Herkimer Co., NY, July 28, 1998, 17 specimens (47.5–80.0 mm SL); NYSM 48304—Moss Lake outlet, Herkimer Co., NY, July 28, 1998, 15 specimens (41.4–54.8 mm SL).

Umbra limi X *U. pygmaea*: NYSM 48783—Manitou Marsh, Putnam Co., NY, September 11, 1998, 4 specimens (32.6–40.2 mm SL); NYSM 55623—Supratidal pool in Manitou Marsh, Putnam Co., NY, October 23, 1998, 31 specimens (36.8–65.0 mm SL).

We compared the mensural and meristic characteristics of the two species using Mann-Whitney U and *t*-tests. We assessed differences among the three groups (*U. limi, U. pygmaea*, and putative hybrids) using analysis of variance (ANOVA), Kruskal-Wallis ANOVA, analysis of covariance (ANCOVA), principal component analysis (PCA), and discriminant function analysis (DFA). The statistical package used was STATISTICA (StatSoft 1984-1995). Measurements and counts were ln-transformed and ratios were arcsine-transformed (Sokal and Rohlf 1981); the transformed data were used in all analyses. ANOVA and the Kruskal-Wallis test were used to examine differences among the group means. Because all mensural variables were highly correlated to standard length (SL), we used ANCOVA to assess the relationships between the other morphometric variables and taxon. Using SL as the covariate and taxon as the independent variable, we compared the residual variance of the other mensural variables among groups. We used PCA to reduce the number of variables in the analysis to two and to examine the relationships among variables. We then used the new variables to assess differences among the three taxa. First, we examined the ln-transformed mensural variables (excluding SL) in a PCA with normalized varimax rotation of the data. We sheared the second component (Humphries et al. 1981). We used the arcsine-transformed ratios (variable/SL) in a similar analysis. Finally, we used the ln-transformed mensural (excluding SL) and meristic data in a DFA to determine which variables best allow us to delineate the groups. The package used performs a canonical correlation analysis that determines the optimal combination of variables so that the first function provides the greatest discrimination among groups and the second function the second greatest discrimination. The two functions are independent. The jackknife technique allowed us to use the counts and measurements from the study sample in the DFA since we did not have these values from an independent sample (Sokal & Rohlf 1981)

Results

We examined 47 *Umbra pygmaea* specimens, 77 *Umbra limi*, and compared them to 35 *Umbra* sp. collected from Manitou Marsh. *Umbra limi* and *U. pygmaea* are very similar species, distinguishable (Table 1) by mean meristic (*t*-test) and morphometric (Mann-Whitney U test) measurements, all of which were statistically significant except for the predorsal length.

TABLE 1. Mean meristic and morphometric measurements comparing *Umbra limi* and *U. pygmaea*. N = 77 and 47, respectively. Mann Whitney U-tests were done on morphometric characters and *t*-tests on meristic ratios.

Measurement	*U. limi*	*U. pygmaea*	Probability
Lateral line scales	33.6	32.4	p = 0.071
Dorsal rays	12.9	11.9	p < 0.05
Anal rays	7.9	7.6	p = 0.005
Predorsal length/SL	1.6	1.7	p = 0.12
Anal base length/SL	10.1	9.6	p = 0.02
Head length/SL	3.1	3.4	p < 0.001
Snout length/SL	4.2	4.5	p < 0.001
Eye diameter/snout	1.0	0.9	p < 0.001
Interorbital width/snout	1.0	0.9	p < 0.001

Using ANOVA, we found significant differences among the groups in all mensural and meristic variables (Table 2). An examination of the means indicated that the observed differences were due to the larger size of *U. limi* specimens. Because the mensural variables were highly correlated with SL (Table 2), the ANOVA may have established significance based on this size relationship. The differences among the meristic characteristics are significant and not related to size. There also were differences ($p<0.05$) among groups in four of the six ratios using the Kruskal-Wallis ANOVA (Table 2). By using the ratios, we moderate, to some extent, the effect of SL. These means show that the differences are not due to the larger *U. limi*, and indicate that there are shape differences in the taxa unrelated to size.

A second way to control for the effect of size is to use ANCOVA, with SL as the covariate. The overall test was significant (Wilks' $\lambda = 0.31$, $p < 0.001$); SL is related to the dependent variables. Differences among the taxa were significant ($p < 0.01$) for each mensural variable except anal-fin base. This also suggests that there are differences in shape among the taxa irrespective of size. *Umbra limi* has a relatively larger head than *U. pygmaea* and the hybrid is intermediate. This relationship holds for all four head measurements (head length, snout length, and interorbital width, and, to a lesser extent, orbit diameter) and predorsal length.

TABLE 2. Comparison of means among *Umbra limi*, *U. pygmaea* and *U. limi* X *U. pygmaea* using ANOVA for measurements and counts and Kruskal-Wallis ANOVA for ratios. The relationship between each mensural variable and standard length (SL) is the correlation coefficient, r. Data are ln- or arcsin-transformed

Variable	Statistic	P	*U. limi*	*U. pygmaea*	Hybrid	r
Standard length (SL)	11.44	0.000	48.6	49.6	56.5	
Predorsal length (PL)	10.50	0.000	30.1	30.1	34.6	0.99
Anal-fin base (AB)	3.98	0.200	5.0	5.2	5.7	0.84
Head length (HL)	18.3	0.000	15.7	14.7	17.7	0.97
Snout length (SnL)	26.74	0.000	3.6	3.3	4.2	0.88
Eye diameter (OD)	17.63	0.000	3.7	3.6	4.1	0.79
Interorbital width (IO)	5.84	0.003	4.0	3.7	4.2	0.86
Dorsal rays	36.09	0.000	12.0	11.9	12.9	
Anal rays	35.34	0.000	7.0	7.6	7.9	
Lateral scales	21.59	0.000	32.2	32.4	33.6	
PL/SL	6.87	0.032	0.62	0.61	0.61	
AB/SL	4.17	0.124	0.10	0.11	0.10	
HL/SL	44.32	0.000	0.32	0.30	0.31	
SnL/SL	28.59	0.000	0.07	0.07	0.07	
OD/SL	5.29	0.071	0.08	0.07	0.07	
IO/SL	35.50	0.000	0.08	0.08	0.07	
Sample size			77	47	35	

The first two principal components explain 90% of the variance in the data (Table 3). Separation of the taxa is incomplete, but visible (Fig. 2A). Individuals of *U. limi* tended to have higher, often positive scores on PCA2 whereas the scores of *U. pygmaea* were generally negative. The hybrids are scattered throughout. All variables had positive loadings on PCA1, with snout length having the highest loading. PCA1 explained 82% of the variation in the data. This component can be interpreted as a generalized size component (Jolliffe 1986), however when the component scores are plotted against SL some separation among the groups emerges (Fig. 2B). This suggests that some shape information is present in PCA1, i.e., the taxa differ in shape at similar life stages. The second principal component explains 8% of the variation in the data and anal-fin base is the characteristic with the highest loading, which is negative. This component also has characteristics of a size component (Pimentel 1979). When the arcsine-transformed ratios, in an attempt to reduce the influence of SL, are used in the analysis, slightly better separation among the groups is achieved (Fig. 2C). The combination of these two principal components accounts for 59% of the total variance (Table 3). Head length/SL and snout length/SL have high positive loading on the first component; anal-base length/SL has a high positive loading and predorsal length/SL loads with a high negative score on the second component. The sheared PCA2 when plotted against PCA1 offers little more discrimination (Fig. 2D). In short, the PCA suggests that the two species, based on their morphometrics, are very similar. Despite their similarity, the mensural characteristics can separate the two species into two slightly overlapping groups. Characteristics of the hybrid are intermediate and the differences are related to changes in shape that are not the result of changes in size.

TABLE 3. Loadings associated with mensural and meristic characteristics of *Umbra limi*, *U. pygmaea* and *U. limi* X *U. pygmaea* from New York populations used in Principal Components and Discriminant Function Analyses. SL is standard length.

Variable	Principal Component			Discriminant Function			
			Sheared	Standardized		Raw	
	PC1	PC2	PC2	Root 1	Root 2	Root 1	Root 2
Predorsal length (PL)	0.201	0.009	0.022	1.179	3.316	6.02	16.94
Anal-fin base (AB)	0.483	-0.776	-0.744	0.263	0.728	1.11	3.08
Head length (HL)	0.243	0.061	0.075	-2.247	-3.734	-12.76	-21.21
Snout length (SnL)	0.595	0.614	0.647	-0.642	0.166	-3.36	0.87
Eye diameter (OD)	0.326	0.102	0.121	-0.226	0.267	-1.73	2.04
Interorbital width (IO)	0.455	-0.089	-0.061	1.234	-0.497	6.59	-2.66
Dorsal rays				-0.548	-0.094	-9.29	-1.59
Anal rays				-0.262	0.594	-3.76	8.52
Lateral scales				-0.453	0.192	-12.45	5.27
Constant						85.04	-36.63
% variance explained	82.0	8.4		75.7	24.3		
PL/SL	0.050	-0.771					
AB/SL	-0.032	0.723					
HL/SL	0.865	-0.178					
SnL/SL	0.755	-0.252					
OD/SL	0.577	0.230					
IO/SL	0.599	0.500					
% variance explained	33.6	25.3					

Because PCA suggested that we had three groups, although very closely related, represented in the data, we entered nine variables into a forward stepwise discriminant function analysis to assess whether the groups were different. Both discriminant functions 1 and 2 were significant (χ^2 = 255 and 80, respectively, $p < 0.005$). The first discriminant function is weighted most heavily by head length and, to a lesser extent, interorbital width and predorsal length (Table 3). This function also accounts for 76% of the discriminatory power of the analysis. Head length and interorbital width make the greatest contribution to the second function as well, which accounts for the remaining 24% of the variance. The first discriminant function largely separated *U. limi*, with negative scores, from *U. pygmaea* and the hybrids, which have positive scores. The second function discriminates between the hybrid, with negative scores, and the two species, which generally have positive scores (Fig. 3).

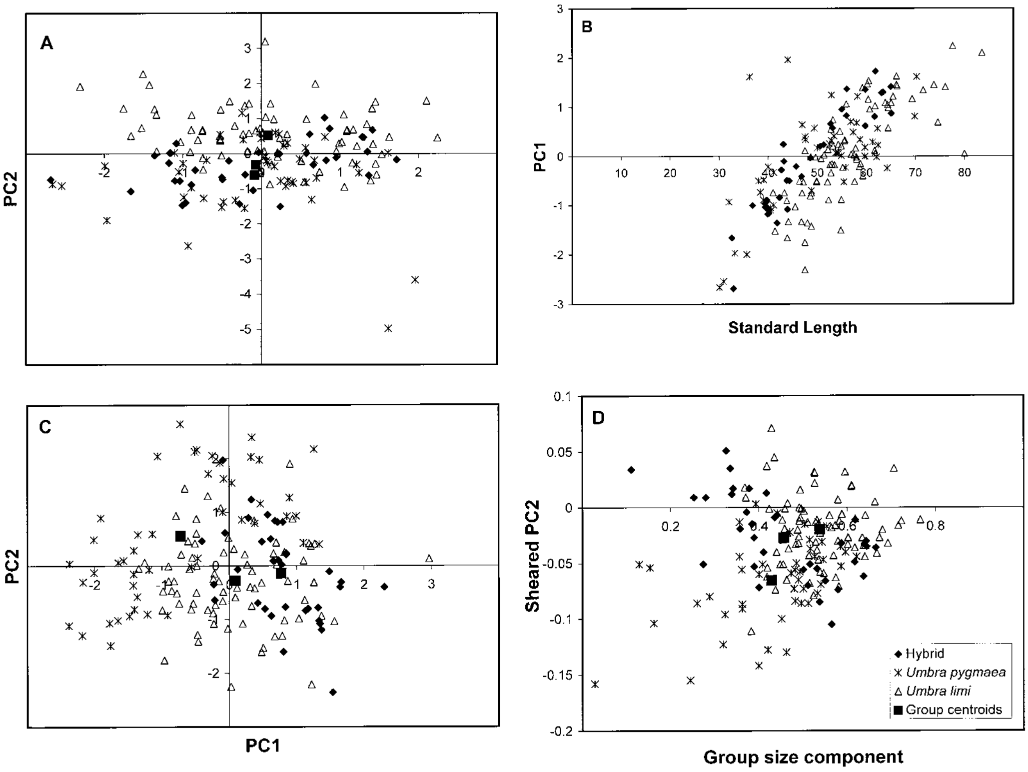

FIGURE 2. Principal component analysis of New York specimens of *Umbra pygmaea* (asterisk), *U. limi* (clear triangles), and the hybrid specimens (solid diamonds). Group centroids are identified by solid squares. **A**. PC1 plotted against PC2. **B**. PC1 plotted against standard length (SL). **C**. PC1 plotted against PC2 when analyzing arcsine-transformed ratios (see Table 1). **D**. Group size component (PC1) plotted against sheared PC2.

The discriminant function correctly classified 89% of the individuals used in the study (Table 4). Hybrid individuals were the ones most likely to be misclassified and only 79% were correctly assigned. Separation of the two species was much better, with only 4 individuals placed into the wrong species. The results were similar using the jackknife technique: 85% of the individuals were assigned to the correct group (Table 4). This suggests that the bias in estimating these statistics resulting from using the values of our study sample in the DFA is low.

We interpret these data as demonstrating hybridization between these closely related species in Manitou Marsh. The tidal Hudson River is the only place where the range of these species overlaps and therefore the only place where hybridization could occur.

TABLE 4. Actual and predicted group membership, based on discriminant analysis of *Umbra limi*, *U. pygmaea* and *U. limi* X *U. pygmaea* from New York populations. Shown are both jackknifed and raw data. The difference between the jackknifed and raw analysis was low, a 4% difference in the number of individuals placed in the correct group.

Jackknifed Group	Actual Group	% Correct	Hybrid	Predicted Group *U. pygmaea*	 *U. limi*
Hybrid	35	83	29	4	2
U. pygmaea	47	83	3	39	5
U. limi	77	87	3	4	67
Total	159	85	38	47	74
Raw Data					
Hybrid	35	78	26	4	3
U. pygmaea	47	85	3	40	4
U. limi	77	96	3	0	74
Total	159	89	32	44	81

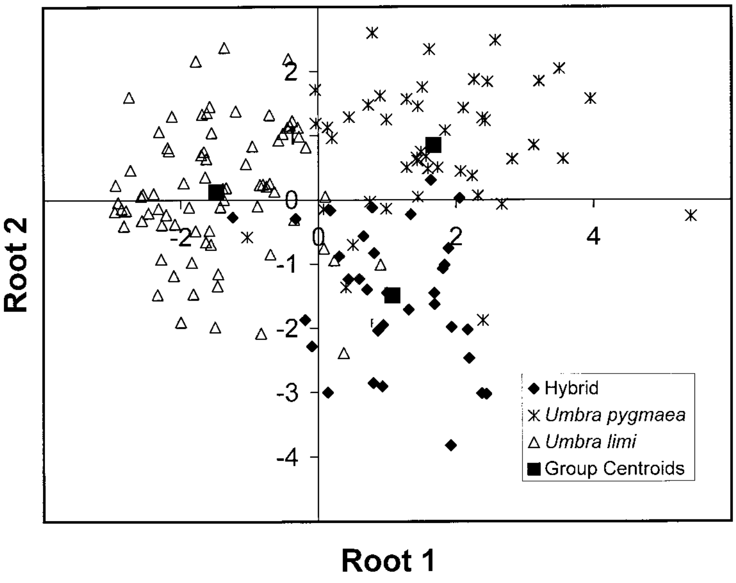

FIGURE 3. Discriminant function analysis of New York specimens of *Umbra pygmaea*, *U. limi*, and the hybrid specimens.

Designation of Neotypes for *Umbra pygmaea* and *U. limi*

Eschmeyer (1998) indicated that there is no known holotype for *U. limi* and that the type(s) of *U. pygmaea* are in the New York State collection, whereabouts unknown.

Recent collecting in the type locality, Sparkill Creek (Stevens and Schmidt 1993, J. Rosko, St. Thomas Aquinas College, *pers. comm.*), has failed to locate *U. pygmaea*. The most recent specimens we have seen are from 1977 (NYSM 52430). *Umbra pygmaea* appears to be extirpated from the type locality, probably due to changes related to urbanization of the watershed.

Although we did not feel it necessary to examine types for this study, the original type specimens of both species are lost or their disposition is unknown. This study is the first alpha-level taxonomic paper to discuss both species and we felt that rectifying at least part of the issue of missing type specimens is appropriate here.

The original descriptions of both species (Kirtland 1840, DeKay 1842) are cursory and do not provide enough information to allow an objective appraisal or, for that matter, identification of either species. The discipline has regarded both species as distinct and identifiable because they were geographically isolated. The two species, which are similar in appearance, are now sympatric in the lower Hudson River drainage, New York, and they now hybridize. Therefore, we designate neotypes at this time because a clear description of each parental species is needed to fix the taxonomic status of both nominal taxa to current usage.

***Umbra pygmaea*-Eastern Mudminnow**

Neotype (Fig. 4)

NYSM 1405, adult, 84.6 mm SL, Sparkill Creek, near Piermont, Rockland County, New York, 1855, S.F. Baird.

Paratopotypes

NYSM 56472, adults, 2 specimens taken with neotype, 84.6–85.4 mm SL. NYSM 14319, adults, 4 specimens, 31.0–42.4 mm SL, Sparkill Creek, downstream of Palisades Interstate Parkway, about 1 km south of the village of Sparkill, Rockland County, New York, June 1978, C.A. Beebe. NYSM 52430, adults, 3 specimens, 35.9–42.1 mm SL, Sparkill Creek, about 100 m downstream of Palisades Interstate Parkway, about 1 km south of the village of Sparkill, Rockland County, New York, 23 July 1977, C.A. Beebe, E. Kiviat, R. St. Pierre.

Diagnosis

Umbra pygmaea is one of three members in the genus *Umbra*, in the family Umbridae. All workers agree that *Umbra* is monophyletic, with the European Mudminnow, *U. krameri*, as the sister species to the two North American species. However, the relationships among the esocoid fishes is controversial (Nelson 1994 for review; López et al. 2004). *Umbra pygmaea* and *U. limi* are very similar in appearance based on morphometrics and meristics. *Umbra pygmaea* tends to have a snout that is shorter than its eye diameter. Its caudal peduncle depth is usually greater than 60% body depth, although this measurement is greatly affected by individual condition. The color pattern of *U. pygmaea* is its most distinctive feature; it has dark, longitudinal stripes separated by lighter stripes of equal or slightly greater depth. There are usually more than 8 stripes on each side. It differs from *U. krameri*, which lacks a prominent vertical black bar at the end of the caudal peduncle, has a mandibular lateral line with two pores (absent in *U. pygmaea*, Nelson 1972), and tends to have more dorsal rays (Lelek 1987). It differs from *U. limi* in color pattern and usually in the relative length of its snout.

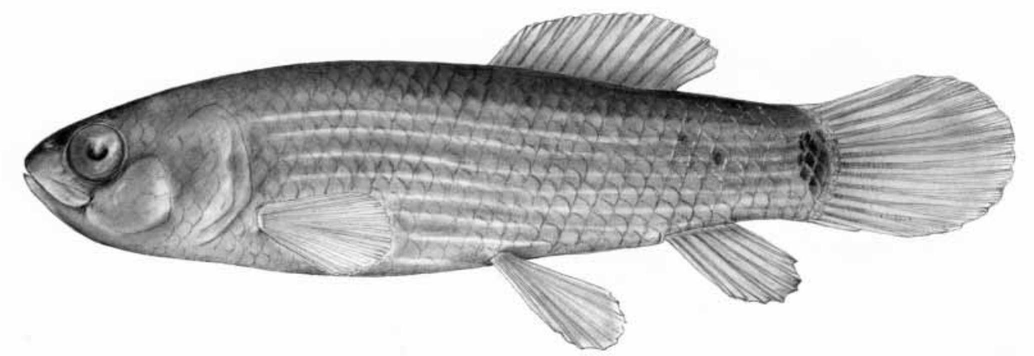

FIGURE 4. Illustration of the neotype of *Umbra pygmaea* (NYSM 1405), 84.6 mm SL.

Description

This is a robust, compact fish, body terete forward, tapering to being slab-sided in the caudal peduncle region. Dorsal profile is slightly arched and the ventral profile is almost flat. Deepest part of the body is just anterior to the dorsal-fin origin, at about 25% SL (see Table 5 for means and ranges of all measurements). Caudal peduncle depth is about 15% SL, so the body profile varies little. Caudal peduncle is longer than deep. Dorsal-fin origin is about 60% SL; anal-fin origin about 70% SL; however, both fins extend back to about 80% SL, so that the insertion of the anal fin is below the midpoint of the dorsal fin. Caudal fin is rounded. Pectoral fins are thoracic and ventral; pelvic fins are abdominal and ventral. The body is entirely scaled, with modified scales encroaching onto the caudal rays.

The head is about 30% SL. The postorbital length is slightly greater than 50% head length (HL). The snout, at 20% HL, is blunt, relatively short, and usually its length is less than the orbit diameter. General shape of the head is conical, with greatest depth posterior, tapering to snout. Eyes are dorsal. Mouth is terminal, horizontal and non-protractile. There are teeth on the premaxillary, dentary, vomer and palatine. Paired nostrils are on the snout anterior to the eyes, each has simple incurrent and excurrent openings. Head is scaled; only the chin, anterior part of the snout, and gular and branchiostegal areas are free of scales. Cephalic lateral line system comprises supraorbital, infraorbital, temporal and preopercular canals, each with relatively few pores. All canals are separate. The supraorbital canal is branched and has four pores; the anterior pore is near the excurrent nostril opening, the third pore is on a branch, the posterior pore is posterior to the orbit and very near the anterior pore of the temporal canal. The infraorbital is Y-shaped, has three pores, is anterior of the orbit and does not extend below the orbit. The temporal canal has two pores, the anterior pore near the terminus of the supraorbital canal, the posterior pore just above the terminus of the preopercular canal. The preopercular canal is branched and has four pores. The anterior pore is below the mid-point of the eye, the second and third pores are on branches and the fourth pore is just below the temporal canal. Pitlines are numerous (see Nelson (1972) for details). The operculum is rounded, relatively large and has a flap of skin along its entire margin; its angle is slightly obtuse. The preoperculum is right-angled and is free only at its angle. The four or five branchiostegal rays are short and thick. Gill membranes are free from the isthmus.

All fins have convex margins. Caudal fin is rounded and symmetrical with 16–18 total rays, 10–12 branched. Ventral and dorsal procurrent rays present. The 12–14 dorsal fin rays are progressive, although the posteriormost rays may be shorter that those immediately anterior. Anal fin typically has 9 rays with the longest rays in the middle. Pectoral fin insertion is just posterior to angle of operculum and its base is small and oblique. Pectoral fin rounded, slightly asymmetrical, with 13–14 rays. Usually both pectoral fins have the same number of rays and the middle rays are longest. Pelvic fin insertion is just anterior to dorsal fin origin. There are six pelvic rays with middle rays longest.

Scales are cycloid. Scales have diffuse foci, lack radii, and ridges are not concentric (Daniels 1996). No modified lateral-line scales. Lateral series counts range from 32–34 scales. There are 12–13 transverse scale rows.

Dorsum dark brown, venter light tan or cream. There are several dark, usually more than eight, thin stripes that run the length of the body, each is separated by a light stripe of equal or greater width. There is a prominent vertical dark bar at the distal edge of the caudal peduncle. Head is dark; operculum is heavily pigmented; cheek is lighter than operculum. The cheek is framed by either an oblique, pigment-free line just below the eye or by an inverted "V" without pigment that includes the suborbital lateral-line canal and a second line that parallels the preopercular canal. The opercular flap is lightly pigmented. The proximal edge of the caudal fin is also heavily pigmented. Fins often have a weak red or maroon tint in life.

Comparison to original description

DeKay (1842) described *Umbra pygmaea* as *Leuciscus pygmaeus*, the "pigmy dace", based on specimens that were no larger than 1 inch (25.4 mm) collected from vicinity of Tappan, Rockland County, New York (Fig. 5). Although he is clearly describing the species recognized today as *Umbra pygmaea*, there are several errors in the text and figure (Fig. 134, DeKay 1842). The original description notes that a lateral line is present, that teeth are absent, and nostrils are inconspicuous. However, it is DeKay's descriptions of the fins that are most puzzling. The caudal fin is described as lanceolate and is figured as long and tapering. The pelvic fins are described as filiform (although not illustrated as such). The dorsal fin is described and illustrated as emarginate. He described the vertical fins as annulate, which is difficult to understand unless he was referring to the structure of the rays. The illustration is labeled as "Nat Size", but measures 1.5 inches in contradiction to DeKay's statement of maximum size.

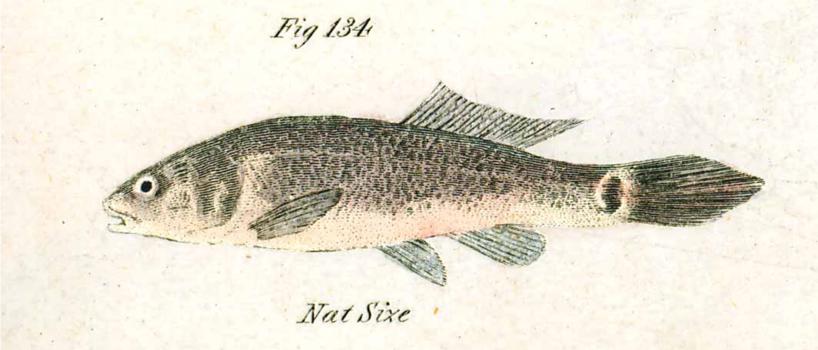

FIGURE 5. Original illustration Plate 42, Fig. 134 of the holotype? of *Leuciscus pygmaeus* from DeKay (1842). The drawing labelled "*Nat Size*" is 29 mm SL, 37 mm TL.

Etymology

When James DeKay (1842) described this species, he noted that this was the smallest of the North American Cyprinidae. So, he named them after the Pygmaioi (Latin Pygmaea), who are, in Greek mythology, a diminutive, dark-skinned tribe that lived on the shores of the River Okeanos and who were tenacious in fighting a never-ending battle with cranes. DeKay probably knew his mythology well and thought the name appropriate for several reasons: pygmaea refers to the small size of the fish, its dark coloration, and its tenacity for life, DeKay (1842) having mentioned that they are "frequently left in shallow pools dried up by the sun".

Umbra limi-Central Mudminnow

Neotype (Fig. 6)

NYSM 56455, adult, 58.8 mm SL, Bull Creek, an upland tributary to Yellow Creek, upstream of Pine Lake, south of Poland, Mahoning County, Ohio, 1 April 2004, R.A. Daniels, R.E. Schmidt, T.O. Matson.

Paratopotypes

NYSM 56456, adults, 16 specimens taken with neotype, 46.4–58.3 mm SL.

Paratypes

NYSM 1309, adults, 2 specimens, 62.0–67.9 mm SL, Lake Champlain, at Burlington, Chittenden County, Vermont, 1853, Z. Thompson.

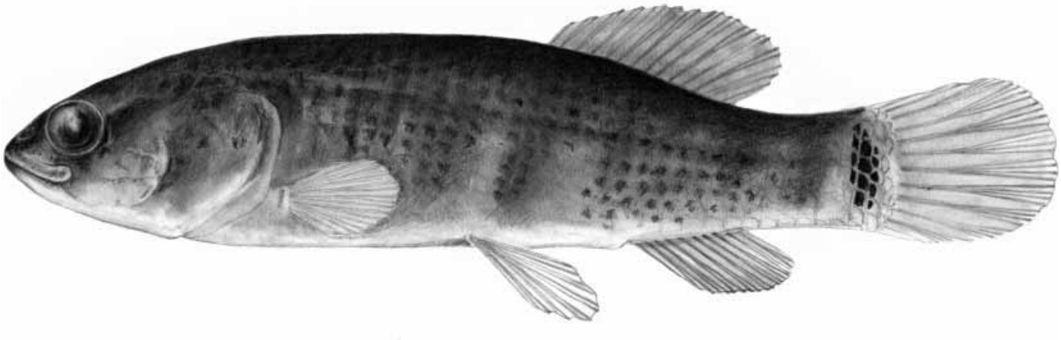

FIGURE 6. Illustration of the neotype of *Umbra limi* (NYSM 56455), 58.8 mm SL.

Diagnosis

Umbra limi is closely related to *Umbra pygmaea* in the family Umbridae (López et al. 2000). *Umbra limi* tends to have a snout that is longer than its eye diameter and its caudal peduncle depth is usually less than 60% body depth. The color pattern of *U. limi* has dark, vertical bars interspersed by lighter areas. There are usually more than 12 bars on each side. It differs from *U. krameri,* which lacks a prominent vertical black bar at the end of the caudal peduncle and has a mandibular lateral line with two pores (absent in *U. limi*, Nelson 1972). It differs from *U. pygmaea* in color pattern and usually in the relative length of its snout.

Description

The similarities between *U. limi* and *U. pygmaea* are more striking than their differences. *Umbra limi* also is a robust, compact fish, body terete forward, tapering to slab-sidedness in the caudal peduncle region. Dorsal profile is slightly arched and the ventral profile is almost flat. Deepest part of the body is just anterior to the dorsal-fin origin, at about 23% SL (Table 5). Caudal peduncle depth is about 13% SL, so there is little change in the body profile from the posterior part of the head to the end of the caudal peduncle. Caudal peduncle is longer than deep. Dorsal fin origin is about 60% SL, anal fin origin about 70% SL, but both fins are coterminal. Caudal fin is rounded. Pectoral fins are thoracic and ventral; pelvic fins are abdominal and ventral. The body is entirely scaled, with modified scales encroaching onto the caudal rays.

The head is about 30% SL. The postorbital length is slightly greater than 50% HL. The snout, at 23% HL, is blunt, relatively short, and usually its length is greater than the orbit diameter. Interorbital distance is also greater than orbit diameter. General shape of the head is conical, with greatest depth posterior, tapering to snout. Eyes are dorsal. Mouth is terminal, horizontal and non-protractile. There are teeth on the premaxillary, dentary, vomer and palatine. Paired nostrils are on the snout anterior to the eyes, each with simple incurrent and excurrent openings. Head is scaled; only the chin, anterior part of the snout, and gular and branchiostegal areas are free of scales. Cephalic lateral line system comprises supraorbital, infraorbital, temporal and preopercular canals, and is identical to that found in *U. pygmaea*. Operculum is rounded, relatively large, and has a flap of skin along its entire margin. Preoperculum is also rounded and is free only at its angle. The four or five branchiostegal rays are short and thick. Gill membranes are free from the isthmus.

TABLE 5. Mensural and meristic values for *Umbra pygmaea* and *Umbra limi*. Neotype for *U. pygmaea* is NYSM 1405; Neotype for *U. limi* is NYSM 56455. Proportions are reported as percentage of standard length.

	Umbra pygmaea			Umbra limi		
	Neotype	Paratypes	mean	Neotype	Paratypes	mean
Sample size	1	9	10	1	18	19
Standard length (mm)	82.2	31.0–85.4	50.5	58.8	46.4–67.9	53.6
Predorsal length	60.8	60.0–63.3	61.3	64.5	58.2–65.1	62.5
Preanal length	73.1	70.0–74.9	72.5	70.6	66.6–72.3	70.2
Head length	28.7	28.7–32.6	30.4	31.1	28.8–34.0	31.0
Postorbital length	16.7	16.4–18.2	17.0	17.7	16.4–19.4	17.6
Snout length	6.2	5.7–7.3	6.6	6.3	6.3–8.0	7.2
Orbit diameter	6.3	6.3–7.8	7.0	5.4	5.4–7.2	6.2
Interorbital distance	7.9	7.0–8.6	7.6	9.0	7.0–9.0	7.8
Pectoral-fin length	15.7	11.3–17.4	14.1	14.1	12.0–16.8	14.3
Dorsal-fin base	22.6	18.7–22.6	20.2	16.8	16.6–21.0	18.8
Anal-fin base	9.1	9.0–11.4	9.8	10.5	8.6–13.1	10.2
Caudal peduncle length	15.7	15.7–20.9	18.7	20.7	1734–21.8	19.9
Caudal peduncle depth	14.7	14.4–16.3	15.3	13.4	12.2–14.2	13.6
Body depth	25.4	21.0–25.4	24.1	23.1	20.5–24.8	22.9
Dorsal-fin rays	13	12–14	13.0	13	13–16	14.4
Anal-fin rays	9	9	9.0	9	8–11	9.5
Pectoral-fin rays	14	13–14	13.8	15	13–16	15.4
Pelvic-fin rays	6	6	6.0	6	6	6.0
Branched caudal rays	12	10–12	11.1	11	9–11	10.6
Lateral scale series	33	32–34	32.8	36	31–36	34.7
Scale rows	13	12–13	12.4	12	12–13	12.8
Branchiostegal rays	4	4–5	4.1	5	4–5	4.2

Fins are similar to those of *U. pygmaea*. Caudal fin is rounded and symmetrical; with 16–20 total rays, 9–11 branched; ventral and dorsal procurrent rays present. The dorsal fin with 13–16 rays, is progressive, although the posteriormost rays are definitely shorter that those immediately anterior. Anal fin with 9–11 rays; the longest rays are those in the middle. Pectoral fin insertion just posterior to angle of operculum, base small, oblique. Fin rounded, slightly asymmetrical, with 13–16 rays. Middle rays longest. Pelvic fin insertion just anterior to dorsal-fin origin. Six pelvic rays present, middle rays longest.

Scales are very similar to those of *U. pygmaea* (Daniels 1996). Lateral series count ranges from 31–36 scales. There are 12–13 transverse scale rows.

Dorsum dark brown or black, venter lighter ranging from cream to light brown. There are several (usually more than 12) dark, vertical dark bars that run the length of the body, each is separated by a lighter area. On some specimens, these bars can be indistinct. There is a prominent vertical dark bar at the distal edge of the caudal peduncle. Head is dark; operculum is heavily pigmented; cheek ranges from as dark as the operculum to much lighter. The opercular flap is lightly pigmented. The proximal edge of the caudal fin is also heavily pigmented. Fins can have a weak red tint. Breeding fish can be very dark with indistinct bars; venter is pink, body with iridescent greens and dark pink areas scattered among the dark pigment.

Comparison to original description

Kirtland (1840) described the Central Mudminnow as *Hydrargira limi* from specimens found in the headwaters of Yellow Creek, Village of Poland, Trumbull County, Ohio. There is no doubt that he described the species recognized today as *Umbra limi*. The description, although brief, is accurate. The original figure (Fig. 7), drawn by Kirtland, is housed at the Bowdoin College library (Moulton 1957).

FIGURE 7. Kirtland's original illustration of the holotype of *Hydrargira limi* from the Library at Bowdoin College.

Etymology

Jared Potter Kirtland was a neophyte ichthyologist when he described *Umbra limi* (Kirtland 1840) and relied heavily on D. Humphreys Storer for guidance and support (Dexter 1980). His descriptions are generally accurate and as thorough as was customary at the time. By placing this mudminnow into the genus *Hydrargira* Lacepède 1803, Kirtland signaled that he believed that this species was closely related to, or was, a killifish. Although there is a typographical error in the presentation of the name, spelled *Hydargira* in the text, it is correctly spelled under the figure. Placing mudminnows in this genus, under Cyprinidae, was customary at the time. DeKay (1842) described *Hydrargira atricauda* (with a typographical error in the presentation of the specific name), the Champlain Minnow, and Thompson (1842) described *Hydrargyra fusca*, also from Lake Champlain. It is curious that DeKay did not recognize a relationship between the Eastern and Central Mudminnow despite their extreme morphological and meristic similarity. Kirtland (1840) noted that the specimens were taken in mud, so the specific name is likely the genitive of the Latin noun limus, translated as slime, mud, or mire.

Biogeography

Umbra pygmaea dispersed into the Hudson drainage during or after recession of the Wisconsinan glacier (Schmidt 1986), reaching its present northernmost locality in the Wallkill River (Smith 1985), a Hudson River tributary. The lack of observations of *U. pygmaea* from the tidal Hudson River raises questions about how hybridization could have occurred. Manitou Marsh is situated 1.7 km north of the narrowest part of the Hudson River estuary (Fig. 1) and directly across the river from Popolopen Brook, a small tributary. The headwaters of Popolopen Brook interdigitate with headwaters of the Ramapo, Wallkill and Moodna Creeks (Woodbury Creek), known to have *U. pygmaea* populations (Smith 1985). Mearns (1898) and Greeley (1937) did not report *U. pygmaea* in Popolopen Brook. Recently (November 1997 & July 1998- J. Beemer, US Military Academy, *pers*. *comm*.), *U. pygmaea* was taken in Johnson Meadow Brook (Fig. 1), a Popolopen Brook tributary. The recent collections of *U. pygmaea* in the Popolopen Brook and lack of earlier specimens from the watershed suggest a recent invasion of the drainage, placing the species very close to Manitou Marsh.

Umbra limi dispersed north and east through the evolving Great Lakes after the Saint Lawrence outlet was opened (Underhill 1986) and eventually into Lake Champlain. Recent (probably 20th century) modifications to the Champlain Canal which connects Lake Champlain with the Hudson River system has encouraged dispersal of fishes through the canal system (Marsden et al. 2000, Plosila and LaBar 1981) and is a likely source of *U. limi* in the Hudson River.

Both species therefore have recently dispersed from their original native distributions, partially due to human modifications of the landscape. These species have retained the ability to reproduce throughout their Pleistocene isolation and hybridization has probably occurred within the last several decades. The fact that these two species hybridize might be expected given their close relationship, however the ability to reproduce is a plesiomorphic character (Rosen 1979) that, *per se*, has no taxonomic significance.

Morphology of the hybrids is very similar to that of the parental species which could indicate introgression. Examination of molecular characters could determine whether introgression has occurred. Rab et al. (2002), Kettler et al. (1986), and López et al. (2000) have provided a basis for further research.

Acknowledgements

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Literature Cited

Beebe, C.A. & Savidge, I.R. (1988) Historical perspective on fish species composition and distribution in the Hudson River estuary. *In*: Barnthouse, L.W., Klauda, R.J., Vaughan, D.S., & Kendall, R.L. (Eds.). *Science, Law, and Hudson River Power Plants.* American Fisheries Society Monograph 4, pp. 25–36.

Cavender, T.M. (1969) An Oligocene mudminnow (Family Umbridae) from Oregon, with remarks on relationships within the Esocoidei. *Occasional Papers of the Museum of Zoology, University of Michigan*, 660, 1–33.

Cooper, E.L. (1983) *Fishes of Pennsylvania and the Northeastern United States.* The Pennsylvania State University Press, University Park, Pennsylvania, 243 pp.

Daniels, R.A. (1996) Guide to the identification of scales of inland fishes of northeastern North America. *New York State Museum Bulletin*, 488, 97 pp.

Daniels, R.A. (2001) Untested assumptions: the role of canals in the dispersal of sea lamprey, alewife, and other fishes in the eastern United States. *Environmental Biology of Fishes*, 60, 309–329.

DeKay, J.E. (1842) *Zoology of New York. Part IV. Fishes.* W. & A. White and J. Visscher, Albany, NewYork, 415 pp.

Dexter, R.W. (1980) The Kirtland-Storer correspondence on Ohio fishes (1838–1845) and a Kirtland-Baird collection of Ohio fishes (1853). *Kirtlandia*, 32, 1–19.

Eddy, S. (1969) *How to Know the Freshwater Fishes.* William C. Brown Company, Dubuque, Iowa, 2nd Edition, 286 pp.

Eschmeyer, W.N. (1998) *Catalog of Fishes*. California Academy of Sciences Special Publication 1, San Francisco, California, 2905 pp.

Greeley, J.R. (1937) Fishes of the area with annotated list. *In* Moore, E. (Ed.), *A Biological Survey of the Lower Hudson Watershed*, Supplement to 26th Annual Report, State of New York Conservation Department, Albany, New York, pp. 45–103.

Humphries, J.M., Bookstein, F.L., Chernoff, B., Smith, G.R., Elder, R.L. & Poss, S.G. (1981) Multivariate discrimination by shape in relation to size. *Systematic Zoology*, 30, 291–308.

Jolliffe, I.T. (1986) *Principal Component Analysis*. Springer Verlag, Berlin, 271 pp.

Kettler, M.K., Ghent, A.W. & Whitt, G.S. (1986) A comparison of phylogenies based on structural and tissue-expressional differences of enzymes in a family of teleost fishes (Salmoniformes: Umbridae). *Molecular Biology and Evolution*, 3, 485–498.

Kirtland, J.P. (1840) Descriptions of four new species of fishes. *Boston Journal of Natural History*, 3, 273–279.

Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E., & Stauffer, J.R., Jr. (1980 *et seq*.) *Atlas of North American Freshwater Fishes*. North Carolina State Museum of Natural History, Raleigh, North Carolina. 854 pp.

Lelek, A. (1987) *The Freshwater Fishes of Europe. Threatened Fishes of Europe*. Volume 9. AULA Verlag, Wiesbaden, 343 pp.

López, J.A., Bentzen, P., & Pietsch, T.W. (2000) Phylogenetic relationships of esocoid fishes (Teleostei) based on partial cytochrome *b* and 16S mitochondrial DNA sequences. *Copeia*, 2000, 420–431.

López, J.A., Chen, W., & Ortí, G. (2004) Esociform phylogeny. *Copeia*, 2004, 449–464.

Marsden, J.E., Langdon, R.W., & Good, S.P. (2000) First occurrence of the brook silverside in Lake Champlain. *Northeastern Naturalist*, 7, 248–254.

Mearns, E.A. (1898) A study of the vertebrate fauna of the Hudson Highlands, with observations on the Mollusca, Crustacea, Lepidoptera, and the flora of the region. *Bulletin of the American Museum of Natural History*, 10, 303–352.

Moore, G.A. (1968) Fishes. *In*. Blair, F.W., Blair, A.P., Brodkorb, P., Cagle, F.R., & Moore, G.A. *Vertebrates of the United States*. McGraw-Hill Inc., New York, New York, pp. 22–165.

Moulton, J.M. (1957) A collection of drawings of fishes ascribed to J.P. Kirtland (1793–1877), in the library of Bowdoin College. *Breviora* 80, 6 pp.

Nelson, G.J. (1972) Cephalic sensory canals, pitlines, and the classification of esocoid fishes, with notes on galaxiids and other teleosts. *American Museum Novitates*, 2492, 1–49.

Nelson, J.S. (1994) *Fishes of the World*. John Wiley & Sons, Inc., New York, New York, 600 pp.

Page, L.M., & Burr, B.M. (1991) *A Field Guide to Freshwater Fishes*. Houghton-Mifflin Company, Boston, Massachusetts, 432 pp.

Pimentel, R.A. (1979) *Morphometrics. The Multivariate Analysis of Biological Data*. Kendall/Hunt Publishing Co., Dubuque, Iowa, 276 pp.

Plosila, D.S. & LaBar, G.W. (1981) Occurrence of juvenile blueback herring in Lake Champlain. *NewYork Fish and Game Journal*, 28, 118.

Rab, P., Crossman, E.J., Reed, K.M. & Rabova, M. (2002) Chromosomal characteristics of ribosomal DNA in two extant species of North American mudminnows *Umbra pygmaea* and *U. limi* (Euteleostei: Umbridae). *Cytogenetic and Genome Research*, 98, 194–198.

Rosen, D.E. (1979) Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History*, 162, 267–376.

Schmidt, R.E. (1986) Zoogeography of the Northern Appalachians. *In*. Hocutt, C.H. & Wiley, E.O. (Eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, Inc., New York, New York, pp. 137–159.

Smith, C.L. (1985) *The Inland Fishes of New York State*. New York State Department of Environmental Conservation, Albany, New York, 522 pp.

Sokal, R.R., & Rohlf, F.J. (1981) *Biometry*. W.H. Freeman & Co., New York, New York, 859 pp.

Statsoft, Inc. (1984–1995) *STATISTICA for Windows: Statistics*, 2nd Edition. StatSoft, Inc., Tulsa, Oklahoma.

Stevens, G., & Schmidt, R.E. (1993) *Preliminary ecological assessment of Sparkill Creek, Town of Orangetown, Rockland County, New York*. Final Report to the Hudson River Defense League by Hudsonia Limited, Annandale, New York, 19 pp.

Thompson, Z. (1842) *Natural History of Vermont*. Charles E. Tuttle Co., Rutland, Vermont, 286 pp.

Underhill, J.C. (1986) The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador. *In*. Hocutt, C.H. & Wiley, E.O. (Eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, Inc., New York, New York,. pp. 105–136.

Werner, R.G. (2004) *Freshwater Fishes of the Northeastern United States*. Syracuse University Press, Syracuse, New York, 335 pp.

Wilson, M.V.H. & Veilleux, P. (1982) Comparative osteology and relationships of the Umbridae (Pisces: Salmoniformes). *Zoological Journal of the Linnean Society*, 76, 321–352.