Status and Distribution of the Hybrid Nocomis micropogon X Rhinichthys cataractae, with a Discussion of Hybridization as a Viable Mode of Vertebrate Speciation

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Abstract: The hybrid *Nocomis micropogon* X *Rhinichthys cataractae* has been known to occur in the upper Monongahela River system from 1899 to present. A comparison of the hybrid with its putative parents in 16 morphometric and meristic characteristics by a hybrid index indicates it is intermediate in six characters, closer to *R. cataractae* in three, and closer to *N. micropogon* in two; five characters are extreme, or outside the range of the means of the parents. *Nocomis micropogon* X *R. cataractae* is unquestionably of hybrid origin; however, it fulfills the characteristics of a morphological species: a definite homogeneous range, clear consistency of characters and success in nature. Hybridization as a mode of speciation in fishes is discussed.

Introduction

Goldsborough and Clark (1908) described *Rhinichthys bowersi* from the "type" taken from Dry Fork at Harman, W. Va., and from cotypes taken from Shavers Fork of Cheat River at Cheat Bridge, W. Va. Raney (1940) collected four specimens of this form below Cheat Bridge in 1935 and redescribed it as a hybrid *Nocomis micropogon* X *Rhinichthys cataractae*. An additional 15 specimens were taken from Shavers Fork in 1975-1976, by members of the West Virginia Department of Natural Resources. The reoccurrence of this hybrid prompted a study to verify its systematic status, range and relative abundance in the upper Monongahela River system. Other objectives of this paper are to provide a morphometric, meristic and descriptive analysis of this hybrid. Additionally, the role of hybridization as a possible mode of sympatric speciation is discussed.

Methods and Materials

Data on previous records of the hybrid were collected via personal communication (R. E. Jenkins, E. L. Cooper), literature review and museum visits. In an attempt to learn more about the present distribution of the hybrid, collections were made at several localities in the Monongahela River system. Fishes were collected by seines and electroshocker, preserved in 10% formalin and placed in 40% isopropanol for permanent storage in the Appalachian Environmental Laboratory Fish Museum.

Fifty specimens of *Nocomis micropogon* and *Rhinichthys cataractae* were collected and compared with 42 hybrids collected prior to 1977. Morphometric characters were measured to the nearest 0.1 mm with dial calipers, using methods given in Hubbs and Lagler (1958) and Raney and Suttkus (1964). A hybrid index was calculated following Hubbs, Hubbs, and Johnson (1943):

$$H = [(X_H - u_1)/(u_2 - u_1)] \times 100$$

where H = hybrid index, X_H = hybrid value, u_1 = value for *N. micropogon* and u_2 = value for *R. cataractae*. Dentition was examined in six hybrid specimens. An index value of 50 denotes exact intermediacy; over 50 indicates that the particular character is closer to *N. micropogon*, and less than 50 indicates a closer affinity with *R. cataractae*.

RESULTS

Distribution and abundance.—Prior to 1975, 14 specimens of the hybrid were known from nine collections (Table 1). With the exception of two Lake Erie collections by Smith and Anderson in 1939 (CU 18281) and Trautman (OSUM 15160) (Ross and Cavender, 1977), all specimens were taken from the Monongahela River system. Additionally, we obtained one specimen of *Nocomis platyrhynchus* X *Rhinichthys cataractae* hybrid from the Greenbrier River, W. Va. During 1975, members of the West Virginia Department of Natural Resources collected 15 specimens of the hybrid from upper Shavers Fork. Six of these were preserved, which we confirmed to be *N. micropogon* X *R. cataractae.* Our efforts in upper Cheat River in 1976 yielded an additional 22 hybrid specimens from Shavers Fork (Fig. 1). The hybrid was present at all but one station above the falls on Shavers Fork (a 3-m falls occurs on Shavers Fork approximately 8 km upstream from Beamis, W. Va.). Our collections of the hybrid represented 5.1% and 6.8%, respectively, of all the *R. cataractae* and *N. micropogon* collected above the falls on Shavers Fork. In 1977, we collected and released three additional specimens of the hybrid from Shavers Fork, preserved one specimen from the Tygart Valley River, W. Va., and one from the Youghiogheny River, Pa., all of the Monongahela River system. Additionally, we have records of three specimens collected from Snowy Creek (Youghiogheny River) in 1977.

Description.—Table 2 summarizes data for 12 morphometric and four meristic characters. Hybrid indices are intermediate (35-65) for six characters, closer to *Rhinichthys cataractae* in three characters and closer to *Nocomis micropogon* in two characters. All hybrid characters were within the range for both parents; however, some mean characters may be considered as "extreme" in that they were outside the range of the mean values determined for the parental species. Head length and snout length [expressed as thousands of standard length (SL)] were greater than the mean for either parent while body length, snout length (expressed as thousands of head length), and snout to dorsal length were lower than the mean for either parent. The mean hybrid index for hybrids collected from the Monongahela system was 50, exclusive of these extreme characters. Dentition was 1, 4-4, 1 for five hybrid specimens and 0, 4-4, 1 for one. *Nocomis micropogon* is typically characterized by 0, 4-4, 0 (Lachner and Jenkins, 1971) while *R. cataractae* is 2, 4-4, 2 (Moore, 1968).

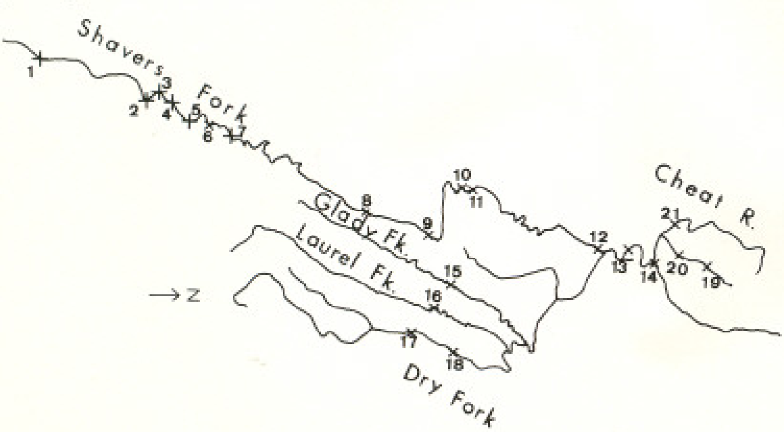

Fig. 1.—Map of the upper Cheat River System denoting stations which were collected in 1976. A + denotes that *Nocomis micropogon* X *Rhinichthys cataractae* was present

TABLE 1.—Collections of *Nocomis micropogon* X *Rhinichthys cataractae* prior to 1975

Locality	Drainage	Date	Number of specimens	Museum no.	Collector
Dry Fork, Harman, W.Va.	Monongahela	30 Aug. 1899	1	USNM 61576**	W. P. Hay
Shavers Fork, Cheat Bridge, W.Va.	Monongahela	25 July 1899	1	USNM 126495***	W. P. Hay
Shavers Fork, Cheat Bridge, W.Va.	Monongahela	25 July 1935	2	UMMZ 109083	E. C. Raney
Minear Run, Co. Rt. 12, W.Va.	Monongahela	1947	3	CU 5699 USNM 199981	
Snowy Cr. below L. Terra Alta, W.Va.	Monongahela	1949	1	CU 32304	R. Barbour
Shavers Fork, Cheat Bridge, W.Va.	Monongahela	10 Sept. 1947	1	CU 24975	E. C. Raney
W. Branch Cazenovia Cr., E. Aurora, N.Y.	Lake Erie	1949	1	CU 18281	Smith and Anderson
E. Branch Chagrin River	Lake Erie	....	..	OSUM 15160	Trautman
Big Meadow Run, Ohiopyle, Pa.	Monongahela	23 June 1965	3	ELC 50*	E. L. Cooper
Flaugherty Creek, Meyersdale, Pa.	Monongahela	19 Oct. 1972	1	ELC 1467*	E. L. Cooper

* E. L. Cooper's collection numbers, housed at Pennsylvania State University
** "Type"
*** Cotype, formerly U. S. Bur. Fish 5314. Other cotypes—SU 20015

Table 2.—Comparison of morphometric and meristic characteristics of the hybrid *Nocomis micropogon* X *Rhinichthys cataractae* with its putative parents

	R. cataractae n = 50		Hybrid n = 42		*N. micropogon* n = 50		Hybrid
	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	index
Standard length, mm	54.2- 95.3	67.4	36.3-121.1	66.0	58.4-165.5	20.3	....
Thousands of SL							
Head length	219 -271	251	247 -208	275	242 -291	272	*
Head depth	116 -150	133	118 -159	145	152 -187	169	.33
Body depth	151 -253	213	176 -236	207	190 -236	218	**
Snout to dorsal	512 -594	535	495 -570	532	490 -570	537	**
Snout to pelvic	368 -500	455	466 -534	495	450 -547	509	.74
Snout length	91 -121	104	93 -131	111	94 -129	110	*
Eye diameter	31 - 53	44	37 - 69	52	38 - 69	58	.57
Least caudal peduncle depth	106 -130	116	98 -125	114	97 -125	108	.25
Thousands of head length							
Snout length	375 -479	417	227 -443	401	342 -484	402	**
Eye diameter	125 -205	174	133 -240	188	144 -240	213	.36
Thousands of snout length							
Eye diameter	283 -536	417	310 -658	472	310 -727	535	.47
Lateral line scales	57 - 70	62.7	44 - 55	48.3	38 - 43	40.5	.65
Scales above L. L.	12 - 16	13.5	8 - 12	10.1	6 - 7	6.4	.48
Scales below L. L.	8 - 13	10.0	6 - 9	7.8	4 - 6	5.1	.45
Numbers of barbels	0 - 2	1.34	0 - 2	1.93	2.0	2.0	.90
Frenum (0 = absent; 1 = present)	1.0	1.0	0 - 1	.66	0	0	.34

* Hybrid value greater than the mean for either parent
** Hybrid value less than the mean for either parent

None of the morphometrics and meristics of the one hybrid from the Lake Erie drainage fell outside the range of the hybrids from the Monongahela River specimens. The one specimen from the Greenbrier River is considered as a *Nocomis platyrhynchus* X *Rhinichthys cataractae* cross since *N. platyrhynchus* is endemic to the New drainage and *N. micropogon* is absent (Lachner and Jenkins, 1971). Only snout length (as a proportion of head length) and number of lateral line scales fall outside of the range of the 42 hybrids from the Monongahela drainage. An overall hybrid index calculated using only this specimen and the 50 *R. cataractae* and 50

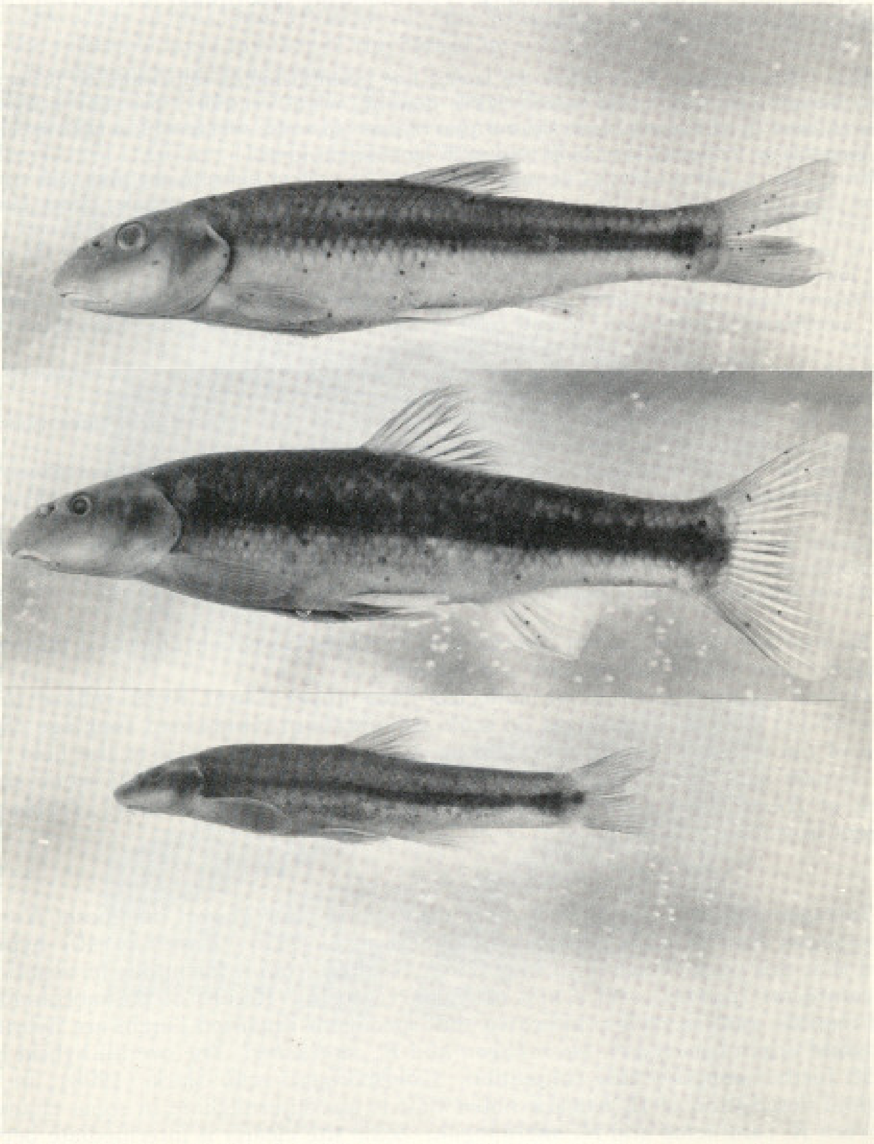

Fig. 2.—Lateral view (top to bottom) of *Nocomis micropogon, Nocomis micropogon* X *Rhinichthys cataractae* and *Rhinichthys cataractae*

N. micropogon is 58. This intermediacy may be explained by (1) the fact that *N. micropogon* and *N. platyrhynchus* are closely related species in respect to characters used in Table 2, or (2) this specimen is indeed *N. micropogon* X *R. cataractae*. Hocutt *et al.* (1978), among others, elaborated on the possibility of a stream capture between Shavers Fork and Greenbrier River.

A comparison of the range of meristic and morphometric data indicates that hybrid characters are as constant as those of putative parents. However, the overall appearance (Fig. 2) of the hybrid is an intermediate mixture of *Nocomis micropogon* and *Rhinichthys cataractae* characters. The following description is based on freshly preserved specimens of the hybrid:

Body. Scales large. Body below the lateral line greenish fading into white on breast, and above lateral line, dark green-brown; black dorsally, white ventrally; posterior margins of scales outlined by chromatophores; central part of exposed scales silvery with a faint green tint due probably to irridophores; caudal peduncle faint yellow-green.

Head. Dark (almost black) dorsally; microtubules present between the eyes and nostrils; lateral line pores visible on the head, 6 - 7 subocular and 1 under the opercle; cheek laterally was evenly speckled with greenish chromatophores; opercle mostly black with a diagonal yellow bar on the lower posterior portion; barbels present at rictus; upper lip yellow along the maxillary; lower jaw faint yellow (not white as on the breast).

Pectoral fins. Melanophores present on leading edge of first ray and along 6 or 7 anterior rays; membranes unpigmented; overall color of fins was yellow toward the body, faint bronze distally

Pelvic fins. Anterior rays with a few micromelanophores; remaining rays contained xanthophores on proximal three fourths; without pigment distally.

Anal fin. Micromelanophores absent from anterior ray, but outlined next three rays; rays contained xanthophores, but were colorless distally; membranes were colorless.

Dorsal fin. Micromelanophores with occasional "bronze" or orange chromatophores outlined branches; membranes contained chromatophores giving proximal half of fin light bronze color.

Caudal fin. Bronze or reddish brown due to pigmentation primarily on the rays; micromelanophores numerous in middle rays and appeared a continuation of the faint lateral band which was intensified as an elongated caudal peduncle spot.

At least two of the smaller hybrids had irridophores which appeared fluorescent along the junction of the occiput and opercles.

Hybrid specimens which we collected from upper Cheat River ranged in size from 40-125 mm SL and, based on scale examination, represented four age classes. Two of the larger specimens captured at station 3 were dissected in the field. The one female had small gonads (Fig. 3), with eggs approximately the same size of those of *Rhinichthys cataractae* females collected at the same time. Testes were present in the male (Fig. 3).

Discussion

Intrageneric and intergeneric hybridization is well known for both *Nocomis micropogon* and *Rhinichthys cataractae* (Schwartz, 1972). Raney (1940) hypothesized that this particular hybrid may have "resulted from a fortuitous fertilization as *R. cataractae* spawned over a nest of *N. micropogon*." Results of the morphological and meristic analysis clearly indicated that specimens discussed herein are hybrids or of hybrid origin between *N. micropogon* and *R. cataractae*. The overall hybrid index of 50 further supports this contention. Goldsborough and Clark (1908), in their original description of *R. bowersi* noted that it was intermediate in some characters between *R. cataractae* and *N. micropogon*. Scale size clearly is intermediate between the two parental types, with little or no overlap in the ranges of lateral line scales, scales above the lateral line and scales below the lateral line (Table 3). The presence or absence of a frenum also clearly places the hybrid between *N. micropogon* and *R. cataractae*. When a frenum is present in the hybrid, it is typically narrower than in *R. cataractae*. In many cases, the lip is bound to the upper jaw only by a thin strip of flesh. Smith (1973) and Nelson (1973) used frenum width when describing *R. cataractae* hybrids. For a complete discussion of the importance of intermediacy in determining natural hybrid combinations, see Hubbs (1955).

There have been many cases in which relatively high incidence of hybridization has been reported. This phenomena has been extremely prevalent in the Cyprinidae. In fact, Hubbs (1955) states that the largest number of freshwater hybrid combinations occur in this family. However, the following discussion will demonstrate that the relatively large number of the hybrid in a restricted area over a period of at least 78 years appears to be unique.

The hybrids *Notropis cornutus* X *Notropis rubellus* and *Notropis chrysocephalus* X *N rubellus* are probably the two most common cyprinid crosses in North America (Gilbert, 1961). Gilbert (1961), Hubbs (1955) and Tsai and Zeisel (1969) attributed this to the simultaneous spawning of the parental species over *Nocomis* nests. These combinations appear to occur, to some extent, whenever the forms are sympatric. The

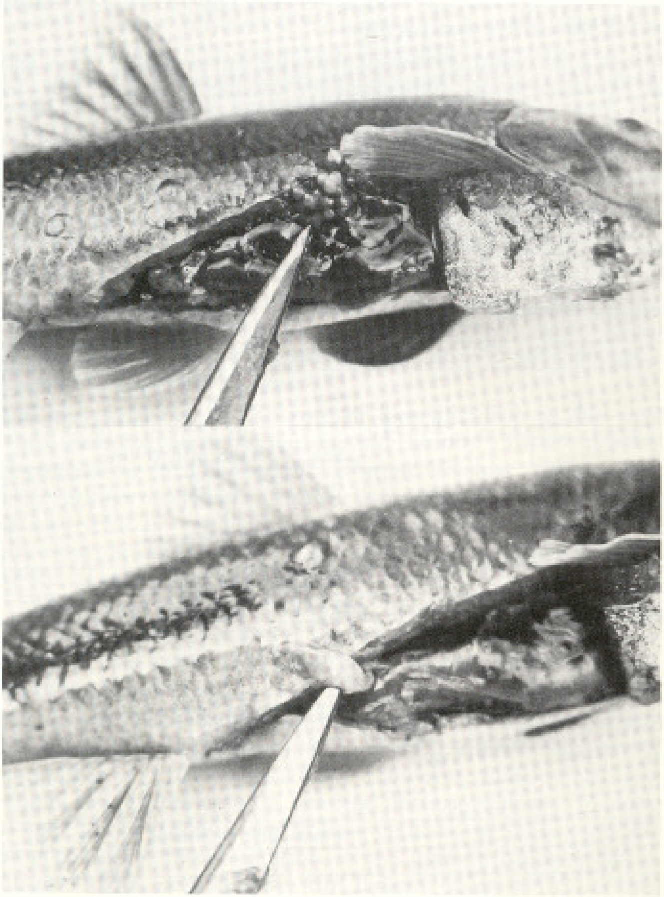

Fig. 3.—View of the gonads of a female (top) and male (bottom) *Nocomis micropogon* X *Rhinichthys cataractae* captured in Shavers Fork at Station 3 during April 1976

fact that there is not a dilution of the characteristics of the parental species is generally attributed to the fact that the offspring are sterile (Gilbert, 1961). Gilbert (1961), based on work by Greeley and Bishop (1932) and Greeley (1934), states that *Phoxinus eos* and *Phoxinus neogaeus* also hybridize frequently when sympatric. These situations differ from our study in the following manner. As stated previously, with the exception of two collections from Lake Erie drainages, all specimens are from the Monongahela River system. However, *Nocomis micropogon* and *Rhinichthys cataractae* occur sympatrically throughout the Appalachian region in the James, York, Rappahannock, Potomac, Kanawha (below Kanawha Falls), Big Sandy and Tennessee rivers (Jenkins *et al.*, 1972). Denoncourt and Cooper (1975) reported both species from the Susquehanna, and Stauffer *et al.* (in press), reported sympatry in the Delaware, and western Chesapeake Bay drainages.

Crowding of spawning fishes has been hypothesized to increase the likelihood of hybridization (Hubbs and Hubbs, 1947; Weisel, 1955; and others). Bailey and Lagler (1937) explained the occurrence of several sunfish hybrids using this hypothesis. The frequent occurrence of the hybrids *Mylocheilus caurinus* X *Ptychocheilus oregonensis* was attributed to crowding (Weisel, 1955). Based on our recent surveys of Shavers Fork, crowding does not appear to be a basis for hybridization of *Nocomis micropogon* and *Rhinichthys cataractae*.

Cohabitation of a rare and abundant fish and the presence of an exotic have both been suggested as catalysts for hybridization (Hubbs, Walker and Johnson, 1943;

TABLE 3.—Scale counts of *Nocomis micropogon* X *Rhinichthys cataractae* and its putative parents

	Lateral line scale															
	38	39	40	41	42	43	44	45	46	47	48	46	50	51	52	53
N. micropogon	1	4	20	18	6	1										
Hybrid							3	2	1	9	6	10	6	3	2	
R. cataractae																

	Lateral line scale																
	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
N. micropogon																	
Hybrid		1															
R. cataractae				1	2	3	8	3	5	7	7	6	3			3	1

	Scales above lateral line					
	6	7	8	9	10	11
N. micropogon	29	21				
Hybrid			2	11	20	9
R. cataractae						

	Scales above lateral line				
	12	13	14	15	16
N. micropogon					
Hybrid	1				
R. cataractae	7	22	10	10	1

	Scales below lateral lines				
	4	5	6	7	8
N. micropogon	2	43	5		
Hybrid			3	12	18
R. cataractae					1

	Scales below lateral lines				
	9	10	11	12	13
N. micropogon					
Hybrid	10				
R. cataractae	20	16	7	5	1

Hubbs and Hubbs, 1947; Weisel, 1955). Hybrids of *Lucania goodei* X *Lucania parva* (Hubbs, Walker and Johnson, 1943), *Catostomus insignis* X *Xyrauchen texanus* (Hubbs and Miller, 1952) and *R. cataractae* X *Richardsonius balteatus* (Weisel, 1955) were attributable to a large abundance of one parent and low abundance of the other. The cross *Couesius plumbeus* X *R. cataractae* (Nelson, 1973, and others) was attributed to introductions. It is doubtful that either of the above phenomena was responsible for the formation of *Nocomis micropogon* X *Rhinichthys cataractae* since both are native to Shavers Fork and are equally abundant. Environmental stress also has been suggested as a cause for hybridization. Water quality in Shavers Fork was adversely affected by timbering and mining in the late 1800s. Today, water quality is generally considered good. It is possible that environmental stress was the principal causative agent of hybridization.

The hybrid was originally described as a species by Goldsborough and Clark (1908) and subsequently redefined as a hybrid by Raney (1940). This situation is not unique in ichthyological literature. *Oxygeneum pulverulentum* (Hubbs and Bailey, 1952), *Notropis kanawha* (Bailey and Gilbert, 1960) and *Notropis germanus* (Hubbs, 1951) were redefined as cyprinid hybrids. More recently, Hopkirk (1974) described a new genus and species *Endemichthys grandipinnis* from specimens originally thought to be hybrids between *Orthodon* and *Lavinia*. In each case, the investigator had to determine if the organisms constitute a species or a hybrid. Wagner (1969) listed several differences between hybrids and species, including the duration of the taxon and the number of generations. Hubbs, Walker and Johnson (1943) also addressed this problem and indicated that hybrids are usually too few to represent an established species, and have characteristics which are clearly intermediate between the putative parents.

Nocomis micropogon X *Rhinichthys cataractae* appears to have characteristics of both a species and a hybrid. Meristic and morphometric characteristics are clearly intermediate between *N. micropogon* and *R. cataractae*. However, there are several generations and the duration of the taxon appears to be continuous at least from 1899 to present. We presently do not have enough information available to make a final determination; however, the possibility of hybridization as a mode for sympatric speciation cannot be ignored.

Probably the best evidence of the role of hybridization in the process of evolution of fishes was demonstrated by Hubbs and Hubbs (1932) when they reported apparent parthenogenesis in a hybrid Poeciliidae. Hubbs (1961) also hypothesized that the genus *Carassiops* may have been of hybrid origin between carp and goldfish. Unlike Hubbs and Hubbs (1932), we have not been able to demonstrate that *Nocomis micropogon* X *Rhinichthys cataractae* can reproduce with genetic consistency. However, it appears that the other characteristics of a vertebrate species are fulfilled in that the hybrid has a definite, homogeneous range, clear consistency of characters and is successful in nature. Certainly, the hybrid fulfills a morphological species concept which has been used historically to describe new fish species without regard for reproductive isolation.

The concept of sympatric speciation dates back to pre-Darwinian days and has been debated by many authors (Mayr, 1963; Hubbs, 1961). Mayr (1963) gives several arguments against sympatric speciation. However, most of the sympatric speciation models which he refutes assume gradual differentiation. If hybridization is a viable mode of speciation, it would not follow classical evolutionary theories; instead, there would be a complete reorganization of the genetic constitution of an organism in one generation. More importantly, the hybrid could be reproductively isolated from both parental species if it were fertile. Thus, hybridization could theoretically effect macroevolution. We are not suggesting that macroevolution replace natural selection as the dominant mode of speciation, but that it may be a viable mode in isolated circumstances. Mayr (1963) refutes hybridization as a viable mode of speciation by stating that it is extremely unlikely that a population of hybrids would be segregated from the parental types until they acquire reproductive isolation. However, if hybridization of *Nocomis micropogon* and *Rhinichthys cataractae* initially resulted from environmental stress or from accidental spawning of *R. cataractae* over *Nocomis* nests, it is possible that the F_1 generation was fortuitously adapted for an unfilled niche or a new environment. Therefore, it would be possible for the hybrids to be ecologically, if not geographically, segregated from the paternal types, thus allowing reproductive isolation to follow if it were not present in the F_1 generation.

It is unclear whether or not the supposed hybrid population of *Nocomis micropogon* X *Rhinichthys cataractae* represents a distinct species. However, this stock appears to be distinct from other cases of frequent hybridization in fishes, either in possible modes of origin or in consistency of characters. The hybrid has been reported from the upper Cheat River since 1899 and at least four age classes were present in the system in 1976. Finally, the morphometric and meristic characteristics of the hybrid are at least as consistent as those of the putative parents. Therefore, it appears that the hybrid has certain characteristics of a vertebrate species in that it is successful in nature, occupies a distinct range and has a clear consistency of meristic and morphometric characteristics. It is suggested that hybridization may be a viable mode of speciation.

It is our present recommendation that the population of *Nocomis micropogan* X *Rhinichthys cataractae* in the upper Cheat Basin be protected until the exact taxonomic status can be determined via karyotyping, electrophoresis and artificial cross-fertilization of the putative parents.

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LITERATURE CITED

BAILEY, R. M. AND C. R. GILBERT. 1960. The American cyprinid fish *Notropis kanawha* identified as an interspecific hybrid. *Copeia*, **1960**:354-357.

——— AND K. F. LAGLER. 1937. An analysis of hybridization in a population of stunted sunfishes in New York. *Pap. Mich. Acad. Sci. Arts Lett.*, **23**:577-606.

DENONCOURT, R. F. AND E. L. COOPER. 1975. A review of the literature and checklist of fishes of the Susquehanna River drainage above Conowingo Dam. *Proc. Pa. Acad. Sci.*, **49**:121-125.

GILBERT, C. R. 1961. Hybridization versus intergradation: An inquiry into the relationship of two cyprinid fishes. *Copeia*, **1961**:181-192.

GOLDSBOROUGH. E. L. AND H. W. CLARK. 1908. Fishes of West Virginia. *Bull. Bur. Fish. Wash.*, **1907**:29-39.

GREELEY, J. R. 1934. Annotated list of the fishes occurring in the watershed. *In:* A biological survey of the Raquette watershed, *Suppl. 23rd Annu. Rep. N. Y. State Conserv. Dep.*, **1933**:53-108.

——— AND S. C. BISHOP. 1932. Fishes of the area with annotated list. *In:* A biological survey of the Oswegatchie and Black River systems. *Suppl. 21st Annu. Rep. N. Y. State Conserv. Dep.*, **1931**:54-92.

HOCUTT, C. H., R. F. DENONCOURT AND J. R. STAUFFER, JR. 1978. Fishes of the Greenbrier River, West Virginia, with drainage history of the central Appalachians. *J. Biogeogr.*, **5**:59-80.

HOPKIRK, J. D. 1974. Endemism in fishes of the Clear Lake region of central California. *Univ. Calif. Publ. Zool.*, **96**:1-135.

HUBBS, C. L. 1951. The American cyprinid fish *Notropis germanus* Hay interpreted as an intergeneric hybrid. *Am. Midl. Nat.*, **45**:446-454.

———. 1955. Hybridization between fish species in nature. *Syst. Zool.*, **4**:1-20.

———. 1961. Isolation mechanisms in the speciation of fishes, p. 5-23. *In:* W. F. Blair (ed.). Vertebrate speciation: A symposium. Univ. Texas Press, Austin.

——— AND R. M. BAILEY. 1952. Identification of *Oxygeneum pulverulentum* Forbes, from Illinois, as a hybrid cyprinid fish. *Pap. Mich. Acad. Sci. Lett.*, **37**:143-152.

——— AND L. C. HUBBS. 1932. Apparent parthenogenesis in nature, in a form of fish of hybrid origin. *Science*, **76**:628-630.

——— AND ———. 1947. Natural hybrids between two species of catostomid fishes. *Pap. Mich. Acad. Sci. Arts Lett.*, **31**:147-167.

———, ——— AND R. E. JOHNSON. 1943. Hybridization in nature between species of catastomid fishes. *Contrib. Lab. Vertebr. Biol. Univ. Mich.*, **22**:1-76.

——— AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. Univ. of Michigan Press, Ann Arbor. 213 p.

——— AND R. R. MILLER. 1952. Hybridization in nature between the fish genera *Catostomus* and *Xyrauchen*. *Pap. Mich. Acad. Sci. Arts Lett.*, **38**:207-233.

———, B. W. WALKER AND R. E. JOHNSON. 1943. Hybridization in nature between species of American cyprinodont fishes. *Contrib. Lab. Vertebr. Biol. Univ. Mich.*, **23**:1-22.

JENKINS, R. E., E. A. LACHNER AND F. J. SCHWARTZ. 1972. Fishes of the central Appalachian drainages: their distribution and dispersal, p. 43-114. *In:* P. C. Holt (ed.). The distributional history of the southern Appalachians. Part III: Vertebrates. Res. Div. Monogr. 4. Va. Polytech. Inst. and St. Univ., Blacksburg.

LACHNER, E. A. AND R. E. JENKINS. 1971. Systematics, distribution, and evolution of the chub genus *Nocomis* Girard (Pisces, Cyprinidae) of eastern United States, with descriptions of new species. *Smithson. Contrib. Zool.* 85:97 p.

MAYR, E. 1963. Animal species and evolution. Belknap Press at Harvard University Press, Cambridge, Mass. 797 p.

MOORE, G. A. 1968. Fishes, p. 22-165. *In:* W. F. Blair, A. P. Blair, P. Brodkorb, F. R. Cagle and G. A. Moore (eds.). Vertebrates of the United States. McGraw-Hill Co., New York.

NELSON, J. S. 1973. Morphological differences between the Teleosts *Couesius plumbeus* (lake chub) and *Rhinichthys cataractae* (longnose dace) and their hybrids from Alberta. *J. Morphol.*, **139**:227-238.

RANEY, E. C. 1940. *Rhinichthys bowersi* from West Virginia, a hybrid, *Rhinichthys cataractae* X *Nocomis micropogon*. *Copeia*, **1940**:270-271.

——— AND R. D. SUTTKUS. 1964. *Etheostoma moorei*, a new darter of the subgenus *Nothonotus* from the White River system, Arkansas. *Copeia*, **1964**:130-139.

ROSS, M. R. AND T. M. CAVENDER. 1977. First report of the natural cyprinid hybrid, *Notropis cornutus* X *Rhinichthys cataractae*, from Ohio. *Copeia*, **1977**:777-780.

SCHWARTZ, F. J. 1972. World literature to fish hybrids with an analysis by family, species and hybrid. *Publ. Gulf Coast Res. Lab. Mus.*, **3**:1-328.

SMITH, G. R. 1973. Analysis of several hybrid cyprinid fishes from western North America. *Copeia*, **1973**:395-410.

STAUFFER, J. R., JR., C. H. HOCUTT AND D. S. LEE. (in press). Zoogeography of the freshwater fishes of the Potomac River. *In:* W. T. Mason (ed.). Biological resources of the Potomac River Basin streams symposium. Interstate Comm. Potomac River Basin.

TSAI, C. AND R. B. ZEISEL. 1969. Natural hybridization of cyprinid fishes in Little Patuxent River, Maryland. *Chesapeake Sci.*, **10**:69-74.

WAGNER, W. H., JR. 1969. The role of taxonomic treatment of hybrids. *BioScience*, **19**:785-789.

WEISEL, G. F. 1955. These new intergeneric hybrids of cyprinid fishes. *Am. Midl. Nat.*, **53**:396-411.

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