

Pararhinichthys, a new monotypic genus of minnows (Teleostei: Cyprinidae) of hybrid origin from eastern North America

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Pararhinichthys, a new genus of North American minnows (Teleostei: Cyprinidae) is described. Its single species was originally described in 1908 as *Rhinichthys bowersi* (Goldsborough & Clark) from specimens collected in Dry Fork of the Monongahela River drainage, Harman, West Virginia. It was subsequently redescribed in 1940 as a hybrid. Assessment of morphological, biochemical, and parasitological data corroborate the hypothesis that the species is valid and consists of a self-perpetuating metapopulation that arose from intergeneric hybridization events between *Rhinichthys cataractae* and *Nocomis micropogon*.

Introduction

Ancestral or contemporary hybridization between species is a process traditionally acknowledged as important in the evolution and adaptation of many plant species (Grant, 1981). The importance of hybridization in the evolution of vertebrate species has been evaluated only recently. While speciation via hybridization is thought to be a rare phenomenon in vertebrates, it has been reported to occur in several groups of fishes. Hubbs & Hubbs (1932) postulated ancestral hybridization in the evolution of the parthenogenetic *Mollienisia formosa* (Girard). Hopkirk (1974) described *Endemichthys grandipinnis* Hopkirk,

from specimens originally described as hybrids between *Orthodon* spp. and *Lavinia* spp. The cyprinid *Barbus alluaudi* Pellegrin was postulated to have arisen through an intergeneric cross between *Barbus somereni* Boulenger and *Varicorhinus ruwenzorii* (Pellegrin) (Banister, 1972). Menzel (1977) hypothesized that *Luxilus albeolus* (Jordan) arose from *Luxilus cornutus* (Mitchill) populations through introgression by *Luxilus cerasinus* (Cope). Echelle & Echelle (1978) provided evidence that the speciation event giving rise to *Cyprinodon pecosensis* Echelle & Echelle was at least partially attributable to introgression with other *Cyprinodon* species. Using biochemical, morphological, and phylogenetic evidence,

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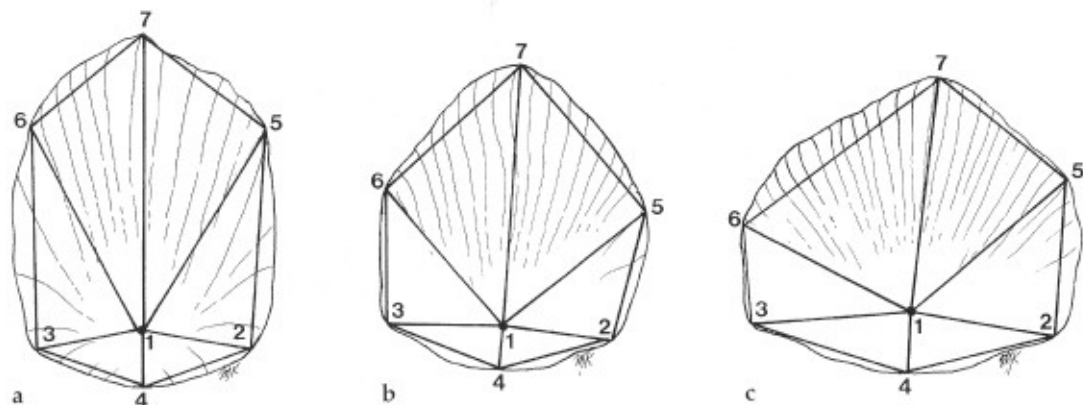


Fig. 1. Scales of *Rhinichthys cataractae* (a), *Pararhinichthys bowersi* (b) and *Nocomis micropogon* (c), denoting points used to establish box-truss network.

Echelle et al. (1983) proposed ancestral hybridization between *Menidia* cf. *beryllina* (Cope) and *Menidia* cf. *peninsulæ* (Goode & Bean) in the evolution of *Menidia clarkhubbsi* Echelle & Mosier. DeMarais et al. (1992) provided evidence that *Gila seminuda* arose through introgressive hybridization and, along with Smith (1992), emphasized the importance of ancestral bouts of hybridization in the evolution of North American freshwater fishes.

The purported 'hybrid' *Nocomis micropogon* × *Rhinichthys cataractae* has been known from the upper Monongahela River drainage since 1899 (Stauffer et al. 1995). This form was originally described as *Rhinichthys bowersi* Goldsborough & Clark from Dry Fork at Harman, West Virginia, (USNM 61576) and from Shavers Fork of Cheat River at Cheat Bridge, West Virginia (USNM 126495) (Goldsborough & Clark, 1908). Subsequently, Raney (1940) collected four specimens of this form from Shavers Fork (UMMZ 109083; CU 5699) and redescribed it as a hybrid, *Nocomis micropogon* (Cope) × *Rhinichthys cataractae* (Valenciennes). Stauffer et al. (1979) argued that *R. bowersi* was not a transient hybrid but was, in fact, reproductively isolated from its putative parents. Employing variability from 43 genetic loci detected using allozyme electrophoresis, Goodfellow et al. (1984) confirmed the distinctiveness of *R. bowersi* as a distinct and independent evolutionary lineage. This study revealed that *R. bowersi* possessed fixed and unique alleles for two enzyme coding loci and serum protein electromorphs not present in either of the putative parental species. Thus, serum protein patterns and

allelic composition from at least seven loci provided unequivocal evidence that allelic variability in *R. bowersi* was not indicative of hybrid intermediacy, as is typically found in transient hybrids. Allelic variability at other loci for *R. bowersi*, however, included both plesiomorphic and apomorphic electromorphs found in *N. micropogon* and *R. cataractae*. Recent studies by Cloutman (pers. comm) concluded that the absence of monogenean parasites, which occur on *N. micropogon*, from the putative hybrid lends credence to the hypothesis that this form is a valid species. The objectives of this paper are to restore this form to specific status, describe a new genus of a North American cyprinid, and give evidence for its origin via introgressive hybridization and anagenetic evolution for apomorphic biochemical and morphological attributes of the species.

Methods

Unless otherwise noted, tests of statistical significance was at $P < 0.05$. Museum abbreviations follow Leviton et al. (1985). Standard methods were employed for mensural and meristic variables following Hubbs & Lagler (1974). Head, body, fin, and scale shape variation among taxa was evaluated using sheared principal component analysis (SPCA) (Humphries et al., 1981; Bookstein et al., 1985). This method is effective in identifying and quantifying shape differences among the taxa/populations independent of size (Reyment et al., 1984). This method was recently used by Stauffer (1991) to distinguish among

Pseudotropheus pursus Stauffer, *P. lanisticola* Burgess, and *P. livingstonii* (Boulenger) from Lake Malawi and by Stauffer et al. (1996) to predict putative parents of the hybrid *P. zebra* (Boulenger) \times *Cynotilapia afra* (Günther). Meristic variation was analyzed using principal component analysis (PCA). Minimum polygon clusters were identified using the first principal component (PC-1) from meristic variation and the sheared second principal component (SPC-2) from morphometric variation. Statistical significance among clusters was determined using MANOVA. If clusters were significantly different on one axis independent of the other axis, Duncan's multiple range test, was used to determine which clusters were significantly different from each other.

Scales used in morphometric comparisons were removed from *N. micropogon*, *R. cataractae*, *R. atratulus*, and *R. bowersi*; scales were sampled from the right side of the body at the tip of the depressed pectoral fin, above the lateral line. If this scale was not present or was damaged, the next closest scale above the lateral line was used. Individual scales were permanently mounted on slides and viewed using a Balplan (Bausch and Lomb) dissecting microscope interfaced with Optical Pattern Recognition System by Biosonics. This system was used to mark seven points on the scale for a truss network (Fig. 1). Skeletal features were examined from cleared and double stained specimens following methods of Dingerkus & Uhler (1977).

Pararhinichthys, new genus

Type species. *Pararhinichthys bowersi* (*Rhinichthys cataractae* \times *Nocomis micropogon*) (Goldsborough & Clark) (Fig. 2).

Diagnosis. Monotypic genus containing *Pararhinichthys bowersi*; morphometric and meristic characteristics presented in Table 1. Hybrid indices summarizing variability of various morphological attributes for *P. bowersi* and its putative ancestral species *R. cataractae* and *N. micropogon* were estimated by Stauffer et al. (1979). The species was found to have intermediate affinities between the ancestral species for six characters, closer affinities to *R. cataractae* for three characters, and closer affinities to *N. micropogon* in two characters.

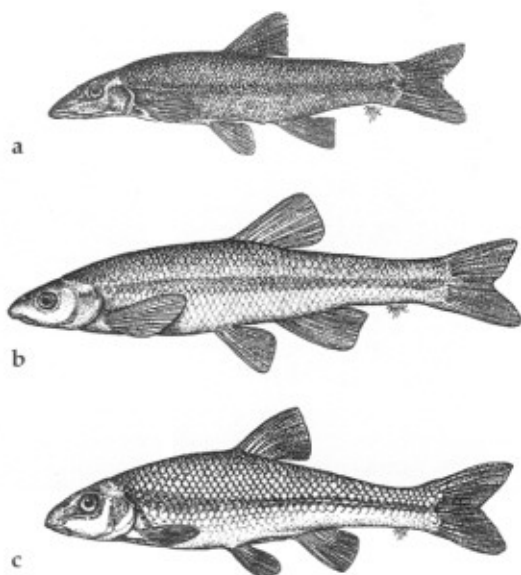


Fig. 2. a, *Rhinichthys cataractae*, 60 mm SL (top); b, *Pararhinichthys bowersi*, 79 mm SL; and c, *Nocomis micropogon*, 67 mm SL. All specimens from Monongahela River drainage, West Virginia.

Comparisons of morphometric and meristic variability of *P. bowersi* with the putative ancestral taxa *N. micropogon* and *R. cataractae* is best accomplished using principle component analysis. Minimum polygons resulting from plotting PC-1 and SPC-2 of all individuals and taxa depict three distinct clusters for *N. micropogon*, *R. cataractae*, and *P. bowersi*, respectively (Fig. 3). While considerable overlap in PC space exists among all three taxa for mensural variables (SPC-2), minimal overlap exists among the taxa for meristic variation (PC-1). Minimum polygons between SPC-2 and PC-1 for all three taxa were significantly different (MANOVA; F values PC-1 = 1105.71, SPC-2 = 426.55; df = 2) and were significantly different from each other along each axis (Table 2) independent of the second axis.

In sheared principal component analysis, SPC-1 represents a size component explaining 90 % of observed variance; SPC-2 depicts shape variance among the taxa for three characters, explaining 6.3 % of the total variance. Variables loading most heavily on SPC-2 include eye diameter (0.77), caudal peduncle depth (-0.38), and head depth (0.35). The first principal component for meristic data explains 65.6 % of the total variance; those variables loading heavily along this

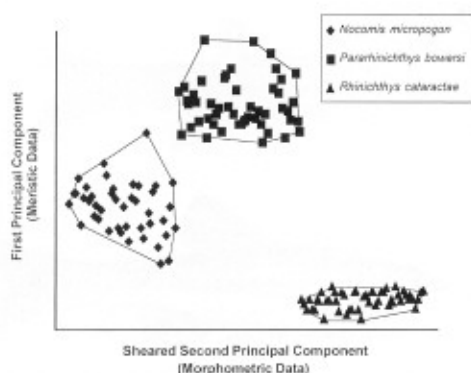


Fig. 3. Minimum polygons of the first principal components of the meristic data versus the sheared second principal components of the morphometric data for *Nocomis micropogon*, *Pararhinichthys bowersi*, and *Rhinichthys cataractae*.

axis are all related to scale size and number and include the number of lateral-line scale rows (0.49), the number of scale rows above lateral line (0.49), and the number of scale rows below lateral line (0.48). Divergence in meristic variables for the three taxa is reflected by the fact that the number of lateral-line scale rows of *P. bowersi*, while intermediate between *R. cataractae* and *N. micropogon*, do not overlap with these taxa. Furthermore, pharyngeal tooth formula of *P. bowersi*

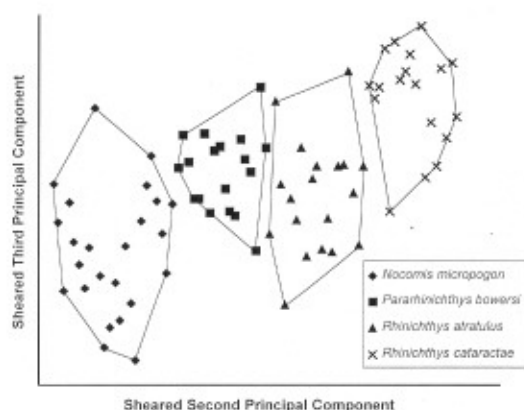


Fig. 4. Plot of individual scores of sheared second principal components and the sheared third principal components of scale shape for *Nocomis micropogon*, *Pararhinichthys bowersi*, *Rhinichthys atratulus*, and *Rhinichthys cataractae*.

(1,4-4,1) differs from that of *R. cataractae* (2,4-4,2) and *N. micropogon* (4-4).

Analysis of scale morphology and shape provides further evidence for distinguishing *P. bowersi* from the putative ancestral taxa, *N. micropogon* and *R. cataractae*. Scales of *P. bowersi* and *N. micropogon* possess basilateral corners (Fig. 1b-c), which are lacking in *Rhinichthys* species. In species of *Rhinichthys*, basal radii are present on scales, while

Table 1. Comparison of morphometric and meristic characteristics of *Pararhinichthys bowersi* (n=42), *Rhinichthys cataractae* (n=50), and *Nocomis micropogon* (n=50).

	mean	SD	range	mean	SD	range	mean	SD	range
Standard length, mm	65.9	17.6	36.2-121.1	67.6	7.4	54.3-95.3	77.0	20.3	58.4-165.5
Head length, mm	18.1	4.7	10.4- 33.8	17.0	1.6	13.5-20.9	21.0	5.4	15.6- 43.5
Percents of standard length									
Head depth	14.5	0.9	11.9-16.1	13.2	0.7	11.7-15.0	16.8	0.7	15.2-18.7
Body depth	20.7	1.3	18.3-23.7	21.3	1.9	15.1-25.4	21.8	1.1	19.0-23.6
Snout to dorsal	53.2	1.6	49.5-57.0	53.5	1.4	51.2-59.4	53.7	1.3	49.1-57.0
Snout to pelvic	49.5	1.5	46.7-53.5	45.5	1.9	36.8-50.0	50.8	1.6	45.0-54.7
Least caudal peduncle depth	0.8	0.2	0.4- 1.5	0.8	0.1	0.6- 1.1	0.8	0.2	0.6- 1.8
Percents of head length									
Eye diameter	18.9	2.2	13.3-24.0	17.3	1.7	12.6-20.5	21.4	2.2	14.4-25.1
Snout length	40.3	2.5	32.7-44.4	41.8	2.3	37.5-47.9	40.2	3.1	34.2-48.4
Counts									
	mode	freq.	range	mode	freq.	range	mode	freq.	range
Lateral-line scales	49	23.8	44-55	60	16.0	57-70	40	40.0	38-43
Scales above lateral line	10	54.8	8-12	13	44.0	12-16	6	58.0	6- 7
Scales below lateral line	8	40.5	6-9	9	42.0	8-13	5	86.0	4- 6
Anal-fin rays	7	92.9	7-8	7	100	7	7	100	7



Fig. 5. Ventral view of the lower jaw of cleared and stained specimens of: a, *Rhinichthys cataractae*, PSU 1809, 56.4 mm SL; b, *Pararhinichthys bowersi*, PSU 82, 56.3 mm SL; and c, *Nocomis micropogon*, PSU 1809, 73.8 mm SL.

these radii are absent from both *N. micropogon* and *P. bowersi* (Fig. 1). Differences in scale shape among these species is illustrated by the minimum polygon clusters formed by plotting the sheared second and third principle components (Fig. 4). Shape of scales of *R. atratulus* and *R. cataractae* appear more similar to each other than the shape of scales of *R. cataractae* to those of *N. micropogon* or *P. bowersi*. Minimum polygon clusters were significantly different (MANOVA; F-values SPC-2 = 283.11, SPC-3 = 29.75), with no overlap between *P. bowersi* and the putative ancestral species. Clusters of each species were significantly different from each other along SPC-2

axis, independent of SPC-3 (Table 3).

Status for *P. bowersi* is further corroborated by assessments of osteological, biochemical, and additional morphological characters. *Pararhinichthys bowersi* differs from *R. cataractae* and *N. micropogon* in the shape of its mandibles. Mandibles (Fig. 5a) of *R. cataractae* are rounded, but at their union medially almost form a straight line. In *P. bowersi* (Fig. 5b) and *N. micropogon* (Fig. 5c), however, the mandibles join to form an acute angle. Goodfellow et al. (1984) reported that the allozyme variability observed in *P. bowersi* did not conform to that expected for hybrids between two putative parental taxa. Allelic products at

Table 2. Duncan's Multiple Range test for the minimum polygon clusters formed by the first PCA of the meristic data and the SPCA of the morphometric data for *Nocomis micropogon*, *Pararhinichthys bowersi*, and *Rhinichthys cataractae*.

minimum polygon clusters for the first principal component (meristic data)			
Duncan Grouping	mean	N	species
A	1.17	50	<i>Rhinichthys cataractae</i>
B	-0.05	42	<i>Pararhinichthys bowersi</i>
C	-1.13	50	<i>Nocomis micropogon</i>
minimum polygon clusters for the sheared second principal component (morphometric data)			
Duncan Grouping	mean	N	species
A	0.09	50	<i>Nocomis micropogon</i>
B	-0.01	42	<i>Pararhinichthys bowersi</i>
C	-0.08	50	<i>Rhinichthys cataractae</i>

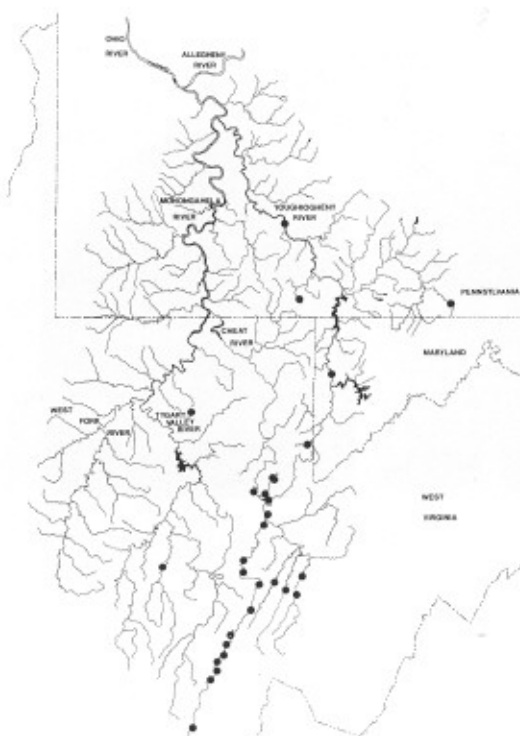


Fig. 6. Localities at which *Pararhinichthys bowersi* has been collected in the Monongahela drainage (see Ross & Cavender (1977) for a site in the Lake Erie drainage).

two loci (Est-B and Gpd-A) were unique to *P. bowersi*. Moreover, when allelic products from tissue extracts of *P. bowersi* were compared directly with a mixture of tissue extracts obtained from *R. cataractae* and *N. micropogon*, the prod-

ucts were not identical, results contrary to what would be expected if *P. bowersi* were indeed an F1 hybrid. In a similar comparative allozyme analysis of hybrid *Campostoma anomalum* × *R. cataractae* with each of the parental species, allelic products for all mixed extracts of the parental species were identical to those observed in the hybrid (Goodfellow et al., 1982). Scales of *P. bowersi* and *N. micropogon* have basilateral corners, no radii, and similar shapes relative to those of species of *Rhinichthys* (Figs. 1 and 4).

Description. Scales relatively large; lateral scale rows 44 to 55; scales rows above lateral line 8 to 12; scale rows below lateral line 6 to 9. Head elongate (24.7-30.8 % of standard length). Barbel small, single, and present in rictus (Table 1). Pharyngeal teeth typically 1,4-4,1.

Etymology. The name *Pararhinichthys* refers to the superficial resemblance of its sole member, *P. bowersi*, to members of *Rhinichthys*.

Distribution. Except for the collection of the species from Lake Erie drainage (Ross & Cavender, 1977; OSM 15160), *P. bowersi* is restricted to the Monongahela River system of the Ohio River drainage in Maryland, Pennsylvania, and West Virginia (Fig. 6).

Prior to 1975, 14 specimens of *P. bowersi* were known from nine collections (USNM 61576 [holotype]; USNM 126495 [paratypes]; UMMZ 109083; CU 5699; USNM 199981; CU 32304; CU 24975; CU 18281; PSU 112; PSU 533) located in the Monongahela River Drainage in West Virginia

Table 3. Duncan's Multiple Range test for the minimum polygon clusters formed by the scale truss measurements for *Nocomis micropogon*, *Pararhinichthys bowersi*, *Rhinichthys cataractae* and *Rhinichthys atratulus*.

minimum polygon clusters for the sheared second principal component			
Duncan Grouping	mean	N	species
A	0.30	18	<i>Nocomis micropogon</i>
B	0.07	23	<i>Pararhinichthys bowersi</i>
C	-0.08	18	<i>Rhinichthys atratulus</i>
C	-0.30	19	<i>Rhinichthys cataractae</i>
minimum polygon clusters for the sheared third principal component			
Duncan Grouping	mean	N	species
A	0.08	18	<i>Rhinichthys atratulus</i>
B	0.01	18	<i>Nocomis micropogon</i>
B	-0.01	19	<i>Rhinichthys cataractae</i>
C	-0.07	23	<i>Pararhinichthys bowersi</i>

and Pennsylvania. In 1975 and 1976, an additional 15 specimens were discovered from Shavers Fork by the West Virginia Department of Natural Resources; Stauffer et al. (1979) reported an additional 22 specimens from Shavers Fork in 1976. In 1977 (PSU 1062) and 1978 (PSU 1156), E. Cooper collected specimens from Shavers Fork, and in 1977, we collected and released three additional specimens from Tygart Valley River, West Virginia, and one from Youghiogheny River, Pennsylvania (Stauffer et al., 1979). Specimens were collected in Two-mile Creek (Warren County, PA, PSU 1233) in 1979. Hendricks (1980) reported one specimen from Youghiogheny River at Hoyes Run, Maryland, one specimen from Youghiogheny River, Connellsville, Pennsylvania, and four specimens from Snowy Creek, a tributary of the Youghiogheny River, West Virginia. In 1986, an additional 20 specimens were collected at six localities in West Virginia (PSU 1788, 1794, 1800, 1808, 1890, 1815).

Discussion

'Botanists recognize the importance of introgressive hybridization in evolution. Our results from *Gila* indicate that zoologists must do the same' (Dowling & DeMarais, 1993: 445-446).

Herein, we describe *Pararhinichthys* as a separate genus, because this evolutionary lineage originated through an intergeneric hybridization event. As discussed by Wiley (1979; 1981: 226-227), intrageneric hybrid taxa are described and classified, with annotation (e.g., species \times species), in the genus containing putative ancestral species. Intergeneric hybrid taxa, however, are no more closely related to one parental species (e.g., one genus) than to another parental species; these species should be classified and properly annotated (e.g., species \times species) in a separate genus. As presented above and discussed below, *P. bowersi* is a valid species, one that is recognizable using any one of many currently accepted species concepts. Furthermore, because of its history of origin, classification of this species in either genus containing its putative ancestral species would misrepresent genealogical relationships. Only through the allocation of this species to a separate genus with annotation can relationships be unequivocally communicated.

Traditionally, hybridization has been viewed largely as a process that retards speciation (Pater-

son, 1993), and leads ultimately to a reduction in diversity through reductive speciation. Recently, however, the significance of introgressive hybridization through additive speciation in the evolution of North American fishes has been a subject of general interest discussed by Echelle et al. (1983), Meagher & Dowling (1991), DeMarais et al. (1992), Dowling et al. (1992), Dowling & DeMarais (1993), and Smith (1973, 1992). Each of these studies has implicated introgressive hybridization as a valid mode of speciation in the evolution of new species. Reticulate speciation is the origin of a new, self-perpetuating evolutionary lineage (species) via hybridization between at least two independent evolutionary lineages (Wiley, 1981). Although a commonly recognized process in plants, it is infrequent among animals, especially vertebrates. Among North American fishes, reticulate speciation is rare, occurring in only a few primarily freshwater families, including the Atherinidae, Cyprinodontidae, Cyprinidae, Goodeidae, and Poeciliidae.

While a relatively rare phenomenon, this mode of speciation is of general interest to the natural sciences for several reasons, including the survival of ancestral species, the evolution of new replicating, coadapted gene complexes in sympatry, the compatibility of possibly distantly related gene pools, and the potential expression of multiple, homologous apomorphic and plesiomorphic attributes in a single descendant species. All of these qualities make lineages derived via reticulate speciation especially attractive for understanding the processes associated with evolution, speciation, ontogeny, and biological diversity. 'Hybrid species' also introduce into otherwise routine phylogenetic analyses complicating factors associated with reticulate evolutionary trees, including aspects of taxa that can preclude our inference of a 'correct' genealogical history due to algorithm incompleteness. Thus, rare species, especially among vertebrates, of hybrid origin are of special interest and importance to resolving plexing questions in several disciplines of the natural sciences.

Recently, Mayden & Wood (1995) and Mayden (in press) evaluated the effectiveness of the various species concepts in taxonomic and systematic studies. The Evolutionary Species Concept (ESC) sensu Wiley (1978) was concluded to represent a primary species concept, and the only concept compatible with all variously recognized valid forms of biodiversity considered species.

While considered the only valid theoretical concept of species, it is non-operational and must be used in association with other 'surrogate' secondary species concepts. Secondary concepts are those compatible with some but not all valid species and cannot always accurately reflect natural patterns of diversity. Among the 21 known secondary species concepts, the phylogenetic species concepts (PSCs) are among the most reliable for identifying diversity consistent with theory underlying ESC; other secondary concepts may be equally valid but are less complicated operationally. The PSCs are the most reliable 'surrogate' concepts to the ESC.

Patterns of variability in an array of morphological and allozyme attributes unequivocally corroborate the hypothesis that *P. bowersi* is a valid species sensu the ESC (Wiley, 1978; Mayden & Wood, 1995; Mayden, 1996). This is supported by the PSC (Cracraft, 1989; Baum, 1992) and most other valid 'surrogate' concepts of species (see Mayden, 1996). *Pararhinichthys bowersi* represents an independent evolutionary lineage of organisms, separate from other cyprinid species, including the sympatric and putative ancestral species *R. cataractae* and *N. micropogon*. It represents an 'irreducible cluster of organisms' (Baum, 1992: 1) as evidenced by several diagnostic characters. These include the number of lateral-line scales, pharyngeal tooth formula, scale and mandibular morphology, and allozymic products from two loci, Est-B and Gpd-A (Goodfellow et al., 1984). These diagnostic attributes denote reproductive isolation as required by the Biological Species Concept, the Hennigian Species Concept, and other surrogate concepts emphasizing isolation, and denote its genetic and morphological distinctiveness as emphasized by the Cohesion, Genetic, Morphological, Phenetic, Polythetic, and Taxonomic species concepts (Mayden, 1996).

The argument that *P. bowersi* is a valid species of hybrid origin is supported by three explicit denotative observations. First, *P. bowersi* has been repeatedly sampled since 1899, a protracted historical documentation for a natural taxon. Adult *P. bowersi* are able reproductively; females sampled during spring months possess ovaries bearing mature eggs and males have well-developed testes (Stauffer et al., 1979). Second, *P. bowersi* possesses diagnostic electromorphs for two genetic loci but also displays both shared derived and plesiomorphic allelic variability for other loci relative to *R. cataractae* and *N. micropogon*. Third,

PC analyses of morphometric and meristic variability reveals intermediate, distinct clusters for *P. bowersi* relative to the putative ancestral species, *R. cataractae* and *N. micropogon* (Fig. 3; see also Stauffer et al., 1979). These observations differ from those by Smith (1973), Raesly et al. (1990), Meagher & Dowling (1991), and others describing the occurrence of transient hybrids between different fish species. In these latter studies, hybrids were typically only observed during short intervals, analysis of variation demonstrated that the hybrids lacked diagnostic characters, and their PC scores, while intermediate between the two putative parents, were usually dispersed within clusters of one or both parental species. Thus, unlike *P. bowersi*, transient hybrids lack diagnostic characters and character variability independently delineating them from their ancestral species.

The presence of basilateral corners, the absence of basil radii, and overall scale shape (Figs. 1 and 4) argue that *P. bowersi* is more similar to *N. micropogon* than to *R. cataractae*. The presence of basilateral corners, however, is a plesiomorphic character (Coburn & Cavender, 1992). Other evidence, however, that *P. bowersi* may be more closely related to *R. cataractae* than to *N. micropogon* derives from parasitological data. Cloutman (1988) hypothesized that the presence of monogenean parasites may be useful in the identification of putative parental species of fish hybrids. Cloutman (pers. comm., 1988) further proposed that if *P. bowersi* is a hybrid it should be parasitized by monogeneans found on *N. micropogon* and *R. cataractae*. *Pararhinichthys bowersi* harbors only *Dactylogyrus rhinichthius*, a species which infests *R. cataractae*. *Dactylogyrus reciprocus*, a species infesting *N. micropogon*, has not been found in *P. bowersi*.

Intergeneric hybridization, although rare when compared to intrageneric hybridizations, has been reported for many cyprinid combinations (Weisel, 1954; Suttkus & Cashner, 1981; Mir et al., 1988; Jenkins & Birkhead, 1994), centrarchids (Schwartz, 1972), flounders (Norman, 1934; Hubbs & Kuronuma, 1942), percids (Schwartz, 1972), as well as many other fish groups. Rjabov (1981) also discusses the viability of some inter-subfamilial cyprinid hybrids. Goldsborough & Clark (1908) recognized the intermediacy in morphological traits of *P. bowersi* but considered it a distinct species; Raney (1940), however, re-described it as a hybrid. Raney also hypothesized that it probably arose via accidental cross fertili-

zation over *N. micropogon* nests, an argument that would support the occurrence of transient hybrids in communities but not one consistent with population numbers and temporal occurrences as observed for *P. bowersi*. Raney's hypothesized mechanism, however, may be viable for the origin of the taxon. *Rhinichthys cataractae* has been observed spawning over *N. micropogon* nests and eggs of both species have been found in a single nest, although simultaneous spawning of these two species in Shavers Fork of Cheat River has never been observed (Cooper, 1980). Intrageneric and intergeneric hybridization is well known for *N. micropogon* (Schwartz, 1972), and probably results from other cyprinid species spawning over the rubble mound nests of *N. micropogon*.

Only a small percentage of animal crosses produce hybrid species (Bullini, 1994); however, based on the evidence presented above, it is clear that hybridization and/or introgression can lead to speciation in particular circumstances. We provide a synthesis of evidence from morphological characters, biochemical assessment, and parasitological data that *P. bowersi* is a valid species. Thus, we place this species in a new genus, *Pararhinichthys*, based on the hypothesis that *P. bowersi* arose from an intergeneric hybridization event involving two distantly related genera.

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