

Lack of Evidence for the Validity of *Rhinichthys bowersi* (Cyprinidae)

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Goldsborough and Clark (1908) described the minnow *Rhinichthys bowersi* from Dry Fork and Shavers Fork of the Cheat River, West Virginia. Raney (1940a) reidentified the holotype of *R. bowersi* as a hybrid *Nocomis micropogon* × *R. cataractae*. Stauffer et al. (1979) reexamined morphometric and meristic characters of *N. micropogon*, *R. cataractae*, and 42 specimens of the putative hybrid collected from the Monongahela basin. They concluded *R. bowersi* to be “unquestionably of hybrid origin” but felt it constituted a “morphological species” based on its distinct range, consistent characters, and apparent success in nature. Stauffer et al. (1979) refrained from assigning taxonomic status to *R. bowersi* due to insufficient data.

Morgan et al. (1984) determined the modal chromosome number of *R. bowersi* and its putative parental species to be the same ($2N = 50$) and thereby uninformative. Goodfellow et al. (1984) reported diagnostic allozymes at two presumed genetic loci and serum proteins that were absent in *N. micropogon* and *R. cataractae*. Citing previous arguments (Stauffer et al., 1979) in addition to their biochemical characters, Goodfellow et al. (1984) recommended that *R. bowersi* be “resurrected as a valid species.” Recently, Stauffer et al. (1997) redescribed *R. bowersi* as a valid species of hybrid origin and placed it in a new genus “*Pararhinichthys*.” The formal restoration of *R. bowersi* to species status was based on the previous studies (Stauffer et al., 1979; Goodfellow et al., 1984) and on additional evidence derived largely from morphometric and meristic variation, scale and jaw morphology, and parasitological data. Stauffer et al. (1997:334) argued that “*Pararhinichthys bowersi* represents an independent evolutionary lineage” and exhibits characteristics emphasized by the Evolutionary Species Concept (sensu Wiley, 1978) and various other species concepts (Mayden, 1997).

We consider the evidence used to support the species status of *R. bowersi* to be inconclusive and, with respect to the electrophoretic data, critically flawed. We agree that *R. bowersi* “arose from intergeneric hybridization events between *R. cataractae* and *N. micropogon*” (Stauffer et al., 1997:327) but argue that it has not been demonstrated that *R. bowersi* represents a self-perpetuating species of hybrid origin (sensu Dowling et al., 1992) or a transient product of on-

going hybridization. We discuss evidence in support of and counter to the species status of *R. bowersi*, compare *R. bowersi* to other vertebrates considered to be of hybrid origin, and suggest what techniques and information are necessary to demonstrate the validity of *R. bowersi* as a distinct taxon. Institutional abbreviations are as listed in Leviton et al. (1985).

Stauffer et al. (1997) described lateral line scale count, pharyngeal tooth formula, and scale and lower jaw morphology as diagnostic for *R. bowersi*. Together with allozymic products from two genetic loci, Stauffer et al. (1997:334) considered these “diagnostic attributes” to “denote reproductive isolation.” Morphology and meristics of *R. bowersi* are consistent with that expected for first filial generation (F_1) hybrids of *R. cataractae* and *N. micropogon* but do not unequivocally demonstrate reproductive isolation of *R. bowersi*. The range in number of lateral line scales of *R. bowersi* (44–55) is intermediate but does not overlap with *N. micropogon* (38–43) or *R. cataractae* (57–70; Stauffer et al., 1997). Intermediacy without overlap in lateral line scale counts has been observed in other minnow hybrids (Greenfield et al., 1973; Poly, 1997a) and is expected for a cross between a species with large (and few) scales and one with small (and many) scales. The pharyngeal tooth formula of *R. bowersi* (typically 1,4,4,1; Stauffer et al., 1997) is intermediate between those typical of *N. micropogon* (4,4) and *R. cataractae* (2,4,4,2; Jenkins and Burkhead, 1994). Intermediacy in pharyngeal tooth formula also is common in minnow hybrids (Greenfield et al., 1973; Ross and Cavender, 1981). Scales of *R. bowersi* are more similar to those of *N. micropogon*: both possess basilateral corners (lacking in *R. cataractae*) and lack basal radii (present in *R. cataractae*; Stauffer et al., 1997). A similar pattern (i.e., hybrid scales lacking basal radii) was reported for hybrids between *R. cataractae* and two other minnows, *Couesius plumbeus* (Nelson, 1966) and *Luxilus cornutus* (Ross and Cavender, 1977), that lack basal radii. The lower jaw of *R. bowersi* more closely resembles that of *N. micropogon* (dentary elements meet at acute angle) than that of *R. cataractae* (dentary elements nearly form straight line at union; Stauffer et al., 1997). In three different cyprinid crosses, Smith (1973) similarly found that jaw elements of hybrids were not intermediate but more closely resembled one of the two parental species.

Stauffer et al. (1997) used principal compo-

nents analysis (PCA) to compare morphometric and meristic variation among *R. bowersi*, *N. microgogon*, and *R. cataractae*. However, their discussion of results (i.e., morphometric and meristic variability of *R. bowersi* is intermediate relative to parental species) was inconsistent with the graph of their PCA analysis (fig. 3, p. 330) that shows *R. bowersi* to be intermediate for morphometric data only. In sum, morphological and meristic characters do not discriminate whether *R. bowersi* represents transient F₁ hybrids or a self-perpetuating species of hybrid origin. Of "diagnostic" attributes discussed by Stauffer et al. (1997), only presence of unique alleles has the potential to demonstrate reproductive isolation and an evolutionary history distinct from its parental species.

Goodfellow et al. (1984) reported that two enzymes, glycerol-3-phosphate dehydrogenase [G3PDH, EC 1.1.1.8; (formerly α -glycerophosphate dehydrogenase)] and esterase (EST-B, EC 3.1.1.-), and some general serum proteins exhibited unique mobilities not present in mixtures of parental tissue extracts. Accordingly, they suggested that *R. bowersi* had diverged genetically since its hybrid origin. However, because at least one of the enzymes (G3PDH) is dimeric (composed of two subunits), it is unlikely that simply mixing parental extracts would allow interchange between parental enzyme subunits to form a hybrid enzyme. For example, Manwell et al. (1963) demonstrated that mixtures of hemoglobins from *Chaenobryttus gulosus* and either *Lepomis cyanellus* or *L. macrochirus* were additive, whereas hemoglobins visualized from known hybrids of *C. gulosus* and the *Lepomis* spp. displayed unique patterns (i.e., combination of allelic products from each parent occurred in vivo). Electrophoretic patterns of mixtures made by Goodfellow et al. (1984) also were additive. To afford a valid comparison to allozymes visualized for *R. bowersi*, Goodfellow et al. (1984) needed to perform in vitro molecular hybridization of parental extracts using either a freeze-thaw technique (Markert, 1963; Wheat et al., 1971) or the technique reported by Millar et al. (1971). These techniques dissociate enzymes with quaternary structure and allow recombination of subunits to form hybrid enzymes (composed of subunits from both parental enzymes) which may exhibit unique mobilities. This was a critical flaw in the Goodfellow et al. (1984) study that, if corrected, might have shown the unique allozymes attributed to *R. bowersi* were indeed hybrid enzymes.

For several enzymes (acid phosphatase, adenylate kinase, and glutamate dehydrogenase), Goodfellow et al. (1984) reported more loci

than are known in diploid cyprinids, and some of the enzymes (e.g., alcohol dehydrogenase) they reported from muscle tissue are not known to occur in muscle of cyprinids (Buth et al., 1991; D. G. Buth, pers. comm.). Because Goodfellow et al. (1984) did not include actual zymograms for enzymes examined (fig. 1, p. 655), their allozyme interpretations cannot be verified. Stauffer et al. (1997) considered the electrophoretic patterns depicted for EST-B to indicate allelic products unique to *R. bowersi*. However, EST-B gel patterns are difficult to interpret because esterase (EST) quaternary structures are often poorly known and several posttranslational modifications can affect EST mobilities (Poly, 1997b). Interpretation of EST patterns must involve inheritance studies, treatment with exo- α -sialidase (neuraminidase, EC 3.2.1.18) to resolve sialic acid-induced heterogeneity, or in vitro molecular hybridization.

Stauffer et al. (1997) commented that the absence in *R. bowersi* of a monogenean parasite (*Dactylogyrus reciprocus*) found in *N. microgogon* corroborates their hypothesis because hybrids inherit an ability to harbor monogenean parasites from both parental species (Cloutman, 1988). However, Cloutman (1988) cautioned that an individual hybrid may harbor parasites from only one parental species or no parasites at all. Thus, absence in *R. bowersi* of a parasite found in *N. microgogon* offers little, if any, support of its specific identity. Parasites can be useful as diagnostic criteria if they are host specific. For example, Paugy et al. (1990) used presence of specific monogenean parasites on their new species of African minnow, *Labeo roseopunctatus*, to reject, in part, an alternative hypothesis that their new taxon was a hybrid. No parasites are known to be unique or specific to *R. bowersi*.

In support of their argument that *R. bowersi* is a valid species, Stauffer et al. (1997:334) noted that it "has been repeatedly sampled since 1899" and thereby exhibits "protracted historical documentation." However, persistence in nature is not a reliable criterion for taxonomic validity. For example, in a sympatric population of closely related minnows *Luxilus chrysocephalus* and *L. cornutus*, ratios of the two species and their hybrid remained stable over a 10-year period, with the hybrid accounting for 2.1% of the three forms collected (Gleason and Berra, 1993). Stauffer et al. (1997:334) considered *R. bowersi* to be "able reproductively" because females "possess ovaries bearing mature eggs and males have well-developed testes." However, it is not uncommon for minnow hybrids to have gonads that appear ripe and normally developed (Raney, 1940b, 1947). It is unknown

whether gametes of *R. bowersi* are viable, no observations of spawning in nature have been documented, and an attempt to induce spawning in the laboratory was unsuccessful (Goodfellow et al., 1984). As Goodfellow et al. (1984) noted, the description of a new species is not required to include data on fertility or reproductive isolation. We argue that such information is necessary when the species is suspected of being an F₁ hybrid and occurs sympatrically with both of its putative parental species.

There is potential for *N. micropogon* and *R. cataractae* to hybridize in nature. Raney (1940a) hypothesized that *R. bowersi* "resulted from a fortuitous fertilization as *R. cataractae* spawned over a nest of *N. micropogon*." Spawning in the nest of another species (nest association) is common in North American minnows and probably accounts for the majority of known hybrid combinations (Jenkins and Burkhead, 1994). Cooper (1980) found eggs of *R. cataractae* in 11 of 16 nests of *N. micropogon* in five streams in the Potomac and Monongahela basins, and eggs of both species were taken together in eight nests. As Stauffer et al. (1997) pointed out, Cooper (1980) did not observe simultaneous spawning of both species; however, eggs of both species collected from a nest in Snowy Creek (Monongahela basin) were close in development indicating that spawning had occurred at nearly the same time.

Specimens of *R. bowersi* not listed in Stauffer et al. (1997) include a paratype (CAS-SU 21035), eight specimens reported by Chipps et al. (1993), and two specimens (INHS 40741, 29667) collected in 1992 and 1993. Stauffer et al. (1997) noted one specimen of *R. bowersi* (OSUM 15160) from outside the Monongahela basin. In addition, Smith (1985) reported a hybrid *N. micropogon* × *R. cataractae* from the upper Allegheny River (AMNH 42055), and Stauffer et al. (1979) reported the same hybrid from a tributary to Lake Erie (CU 18281; incorrectly listed from Monongahela Drainage in Stauffer et al., 1997). Stauffer et al. (1979) also identified a hybrid *Nocomis platyrhynchus* × *R. cataractae* from the Greenbrier River (Kanawha Drainage) that, according to Goodfellow et al. (1984), "may also be *bowersi*." Given the propensity for *N. micropogon* and closely related *N. platyrhynchus* to hybridize with *R. cataractae* in nature, it seems prudent to treat *R. bowersi* as an F₁ hybrid.

Stauffer et al. (1997) noted that speciation via hybridization has been reported for several fishes and cited as examples *Mollienisia formosa* (Hubbs and Hubbs, 1932), *Endemichthys grandipinnis* (Hopkirk, 1974), *Barbus alluaudii* (Banister, 1972), *Luxilus albeolus* (Menzel, 1977), *Cyprinodon*

pecosensis, and the two minnows, *Gila seminuda* (DeMarais et al., 1992). Only two of these examples are biologically similar to *R. bowersi*. Based on the argument of Stauffer et al. (1997), *R. bowersi* is a bisexual (gonochoristic) species that reproduces sexually. The molly, *Mollienisia* (= *Poecilia*) *formosa*, and the silverside, *Menidia clarkhubbsi*, are unisexual (all-female) species (or species complexes) that reproduce clonally via gynogenesis (Turner, 1982; Echelle et al., 1989). The pupfish, *Cyprinodon pecosensis*, and the two minnows, *Gila seminuda* and *Luxilus albeolus*, are bisexual (gonochoristic) species; however, unlike *R. bowersi*, each now occurs sympatrically with only one (*albeolus*) or neither (*seminuda* and *pecosensis*) of its putative parental species (DeMarais et al., 1992; Echelle and Echelle, 1978; Jenkins and Burkhead, 1994). Furthermore, Echelle et al. (1987) found no electrophoretic evidence to support their previous hypothesis for the hybrid origin of *C. pecosensis*. Data available for *L. albeolus* (Menzel, 1977; Buth 1979) and *G. seminuda* (DeMarais et al., 1992) suggest that these taxa originated via introgressive hybridization, the former eventually replacing one of its parental species throughout its range and the latter replacing both.

The nominal species *Barbus alluaudi* and *Endemichthys grandipinnis* are potentially, albeit dubiously, similar to *R. bowersi*. Banister (1972:282) hypothesized that the African minnow, *B. alluaudi*, was a hybrid of sympatric *B. somereni* and *Varicorhinus ruwenzorii* and, in fact, suggested it "unlikely" that *B. alluaudi* was a "good species." Hopkirk (1974) described the minnow *E. grandipinnis* based on 12 specimens from Clear Lake, California. Hubbs (1974) dismissed these specimens as probable hybrids of sympatric *Lavinia exilicauda* and *Orthodon microlepidotus*, and *E. grandipinnis* was not recognized (Robins et al., 1980). Hybridization plays a role in the evolution of some fishes (DeMarais et al., 1992); however, the evidence for *R. bowersi* differs trenchantly from that for other species (e.g., *G. seminuda*) whose hybrid origin has been carefully inferred and whose genetic and reproductive isolation is evident.

Questions concerning the validity of *R. bowersi* parallel those related to the status of the red wolf, *Canis lupus*. The taxonomic status of the red wolf has been argued in terms of a species descended from an intermediate stage in wolf evolution, a hybrid of the coyote, *C. latrans*, and gray wolf, *C. lupus*, and a taxon of hybrid origin (reviewed in Roy et al., 1996). Dispute over its taxonomic validity (and hence, conservation priority) prompted Dowling et al. (1992) to distinguish between a hybrid (individual of mixed

ancestry tracing its origin to the mating of a male and female of different taxa) and taxa of hybrid origin (self-perpetuating groups of individuals of mixed ancestry following an evolutionary trajectory independent from that of their progenitors). This distinction is important because hybrid taxa may be protected under the Endangered Species Act, but a group of hybrids would not "merit protection until it became self-perpetuating and achieved an independent evolutionary track" (Dowling et al., 1992). Analyses of mitochondrial and nuclear (microsatellite) DNA markers strongly suggest that the red wolf is not an ancient lineage of canines experiencing recent introgression but a product of extensive hybridization for which the timing (i.e., pre- vs post-European settlement) remains ambiguous (Roy et al., 1996).

The morphological and parasitological data available for *R. bowersi* and its historical documentation in nature do not discriminate between its status either as a reproductively isolated species or a product of ongoing hybridization. We believe the biochemical evidence of Goodfellow et al. (1984) taken to indicate reproductive isolation of *R. bowersi* is critically flawed and that the "diagnostic" loci need to be reexamined using in vitro molecular hybridization of parental tissue extracts. Finally, because *R. bowersi* is sympatric throughout its range with both parental species, any case for species status must demonstrate that *R. bowersi* is self-perpetuating and has achieved an evolutionary trajectory independent from that of its progenitors. Self-perpetuation can be demonstrated only through observations of spawning and survivability of offspring to sexual maturity. At this point, we believe that *R. bowersi* is best considered as an F₁ hybrid of *Nocomis micropogon* and *Rhinichthys cataractae*.

ACKNOWLEDGMENTS

We thank B. Burr, D. Buth, D. Cloutman, L. Page, E. Wetzel, and three anonymous reviewers for comments and suggestions on improving the manuscript and J. Brawn for statistical advice. Special thanks to B. Brown, D. Catania, and C. Dardia for providing museum records and to B. Sargent for help in obtaining permits. For field assistance in West Virginia, we especially thank J. Armbruster, L. Avella, D. Cincotta, C. Laird, L. Page, and R. Steinberg. Study supported in part by a Herbert Holdsworth Ross Memorial Grant (INHS) to MHS.

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