



## Phylogenetic relationships of *Moxostoma* and *Scartomyzon* (Catostomidae) based on mitochondrial cytochrome *b* sequence data

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A recent phylogenetic study based on morphological, biochemical and early life history characters resurrected the genus *Scartomyzon* (jumprock suckers, *c.* eight–10 species) from *Moxostoma* (redhorse suckers, *c.* 10–11 species) and advanced the understanding of relationships among species in these two genera, and the genealogical affinities of these genera with other evolutionary lineages within the tribe Moxostomatini in the subfamily Catostominae. To further examine phylogenetic relationships among moxostomatini suckers, the complete mitochondrial (mt) cytochrome *b* gene was sequenced from all species within this tribe and representative outgroup taxa from the Catostomini and other catostomid subfamilies. Phylogenetic analysis of gene sequences yielded two monophyletic clades within Catostominae: *Catostomus*+*Deltistes*+*Xyrauchen*+*Erimyzon*+*Minytrema* and *Moxostoma*+*Scartomyzon*+*Hypentelium*+*Thoburnia*. Within the Moxostomatini, *Thoburnia* was either unresolved or polyphyletic; *Thoburnia atripinnis* was sister to a monophyletic *Hypentelium*. In turn, this clade was sister to a monophyletic clade containing *Scartomyzon* and *Moxostoma*. *Scartomyzon* was never resolved as monophyletic, but was always recovered as a polyphyletic group embedded within *Moxostoma*, rendering the latter genus paraphyletic if ‘*Scartomyzon*’ continues to be recognized. Relationships among lineages within the *Moxostoma* and ‘*Scartomyzon*’ clade were resolved as a polytomy. To better reflect phylogenetic relationships resolved in this analysis, the following changes to the classification of the tribe Moxostomatini are proposed: subsumption of ‘*Scartomyzon*’ into *Moxostoma*; restriction of the tribe Moxostomatini to *Moxostoma*; resurrect the tribe Erimyzonini, containing *Erimyzon* and *Minytrema*, classified as *incertae sedis* within Catostominae; retain the tribe Thoburniini.

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### INTRODUCTION

Redhorse (*Moxostoma*, *c.* 10–11 species) and jumprock (*Scartomyzon*, *c.* eight–10 species) suckers (Cypriniformes: Catostomidae) are common inhabitants of temperate aquatic ecosystems of North America. Species of *Moxostoma* typically inhabit larger rivers and streams; *Moxostoma* are distributed east of the

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continental divide, from southern Canada to the Red River of Texas and Oklahoma and throughout the eastern U.S.A. (Scott & Crossman, 1973; Lee *et al.*, 1981; Page & Burr, 1991). Species of *Scartomyzon* typically inhabit riffle habitats in streams to medium rivers, although a few species are found in upper mainstem rivers. *Scartomyzon* exhibits a disjunct distribution, with five species from the south-eastern U.S.A. and three or more species in Texas and Mexico. *Scartomyzon austrinus* (Bean) and *Scartomyzon mascotae* Regan are found on the Pacific slope of Mexico and are the southern-most species of *Scartomyzon*. The two genera are diagnosable based on their lateral-blotch saddle pattern and caudal peduncle scale count [16 in *Scartomyzon*, 12 in *Moxostoma*, although 16 in *Moxostoma (Megapharynx)*; Jenkins, 1970]. Jenkins (1970) noted, however, that caudal peduncle scale counts might be 'labile or historically influenced by species ecology'; he suggested that the naturalness of these genera based on this single character might be 'suspect'.

*Moxostoma* and *Scartomyzon* have been characterized as one of the most 'perplexing' groups of fishes in North America (Robins & Raney, 1956). This characterization was due partly to subtle morphological differences among some species, particularly within *Moxostoma*, a trait of these fishes that led investigators prior to 1900 to misidentify many species and produce multiple species descriptions for some taxa (Robins & Raney, 1956; Jenkins, 1970). While much of the current stability in the classification and nomenclature of these fishes was provided by Hubbs (1930), Robins & Raney (1956), Jenkins (1970) and Smith (1992), questions remain concerning the validity of *Scartomyzon* as a distinct genus (Harris & Mayden, 2001) and phylogenetic relationships among putative sister species in both genera (Jenkins, 1970).

Robins & Raney (1956) examined variation in morphological and colouration characters of *Moxostoma (Scartomyzon)* in an attempt to better diagnose species from the south-eastern U.S.A.; they also speculated on potential phylogenetic relationships among some species of *Scartomyzon*. *Moxostoma ariommmum* Robins & Raney was so morphologically distinct from other *Scartomyzon* that they felt it was of 'uncertain relationships'. *Moxostoma lachneri* Robins & Raney and *Moxostoma rupiscartes* Jordan & Jenkins were considered 'close relatives'; *M. rupiscartes* was also thought to be the 'closest relative' of *Moxostoma cervinum* (Cope). *Moxostoma robustum* (Cope) (= *S. sp. cf. lachneri*) inhabiting rivers from Virginia to Georgia, was considered related to *Moxostoma congestum* (Baird & Girard) ranging from the Brazos River, Texas, south into Mexico. *Moxostoma austrinum* (Bean), inhabiting rivers on both the Atlantic and Pacific slopes of Mexico, was thought to be related to *Moxostoma mascotae* Regan, occupying rivers of the Pacific slope of Mexico. These four species were collectively referred to as the *M. robustum* species group.

Jenkins (1970) provided the first comprehensive revision of *Moxostoma*; he also speculated on genealogical relationships among moxostomatine suckers, which also included *Lagochila*, *Moxostoma (Scartomyzon)*, *Moxostoma (Thoburnia)* and *Hypentelium* Rafinesque. Jenkins recognized two subgenera within *Moxostoma*, *Megapharynx* [containing *Moxostoma hubbsi* (Legendre) and *Moxostoma valenciennesi* Jordan] and *Moxostoma s. s.* Within *Moxostoma s. s.*, *M. sp. cf. poecilurum* was related to *Moxostoma poecilurum* (Jordan), and *Moxostoma duquesnei* (Lesueur) had 'distant affinities' with these two species.

No potential genealogical affinities were noted for the three subspecies contained within *Moxostoma macrolepidotum* (Lesueur). Jenkins (1970) noted both species had distinctive V-shaped lower lips, but did not consider *Moxostoma anisurum* (Rafinesque) and *Moxostoma pappillosum* (Cope) to be 'intimately related', although such a relationship might be inferred from his phylogenetic hypothesis. No comment was provided on potential sister species relationships for either taxa. *Moxostoma collapsum* (Cope), from the Atlantic slope, was synonymized with *M. anisurum*. *Moxostoma carinatum* (Cope) and *Moxostoma erythrurum* (Rafinesque) were considered closely related based on the large anterior head tubercles developed during the breeding season. Jenkins (1970) retained *Lagochila* (Jordan & Brayton) as a distinct genus based on its unique trophic morphology, although he noted its 'ancestral relationship' with *Moxostoma s. s.* Relationships within the subgenus *Scartomyzon* were in agreement generally with Robins & Raney (1956), although Jenkins (1970) speculated that *M. rupiscartes* and *M. cervinum* were closely related based on colouration and morphology; *M. ariommmum* was considered a transitional form between *Moxostoma* (*Scartomyzon*) and *Moxostoma* (*Thoburnia*).

Buth (1978) examined allozyme variation in *Moxostoma* (*Scartomyzon*) and *Moxostoma* (*Moxostoma*) and proposed some phyletic relationships. *Moxostoma ariommmum* was the basal-most taxon within the subgenus *Scartomyzon*. The *M. robustum* species group was considered polyphyletic; *M. robustum* was basal to *M. rupiscartes* plus a clade of *M. lachneri*, *M. cervinum*, *M. congestum*, *M. austrinum* and *M. mascotae*. Within this latter clade, *M. congestum* was polyphyletic, with *M. c. congestum* from the Guadalupe River, Texas, sister to *M. cervinum* plus *M. lachneri*. *Moxostoma c. albidum* was recovered as paraphyletic and was basal to a paraphyletic *M. austrinum* plus *M. mascotae*. Phylogenetic relationships recovered within *Moxostoma* (*Moxostoma*) differed from those proposed by Jenkins (1970). *Moxostoma pappillosum* was the basal-most taxon within *Moxostoma s. s.* *Moxostoma carinatum* was sister to *M. macrolepidotum sensu lato*, rather than *M. erythrurum*, which was sister to *M. anisurum*. *Moxostoma duquesnei* was basal to *M. poecilurum* and *M. sp. cf. poecilurum*, which were not recovered as sister taxa, *contra* Jenkins (1970).

Smith (1992) provided the first comprehensive analysis of catostomid relationships based on 64 taxa and 157 morphological, biochemical and early life history transformation series (Fig. 1). Smith's (1992) analysis produced two equally parsimonious trees of 852 steps (CI=0.35). In this study he elevated *Scartomyzon* out of *Moxostoma*. In his preferred tree *Moxostoma* and *Scartomyzon* were recovered as paraphyletic grades with some species of both genera more closely related to species of the other; furthermore, an unresolved trichotomy was resolved between *Scartomyzon ariommmus* (Robins & Raney), *Thoburnia* and *Hypentelium*. The second topology yielded *Scartomyzon cervinus* (Cope) as sister to an unresolved trichotomy of *S. ariommmus*, *Thoburnia* and *Hypentelium*. These results suggest that some species currently recognized in *Moxostoma* or *Scartomyzon* may be more closely related to other *Moxostoma*, a *Thoburnia* plus *Hypentelium* clade, or form distinct evolutionary lineages. Smith (1992) noted that *Moxostoma* as currently recognized was definable, but not diagnosable; *Moxostoma* was placed in shutter quotes to represent the potential

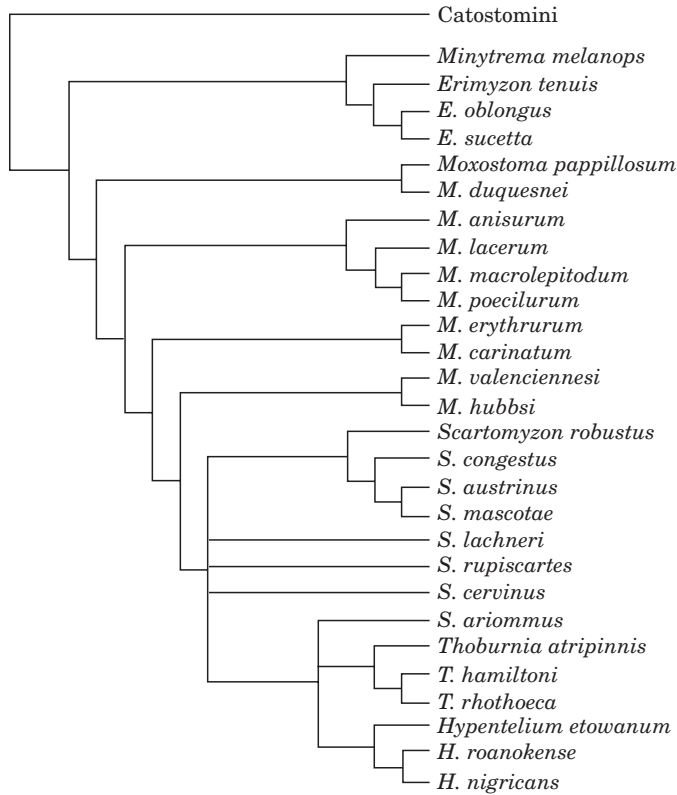


FIG. 1. Simplification of Smith's (1992) phylogenetic hypotheses based on morphological, biochemical and early life history characters.

para- or polyphyletic nature of the genus. Smith (1992) expanded Jenkin's (1970) Moxostomatini to include *Erimyzon* and *Minytrema* as the sister clade to the *Moxostoma* group.

Harris & Mayden (2001) examined phylogenetic relationships among basal-lineages of catostomids based on mitochondrial (mt) SSU and LSU rRNA genes. *Scartomyzon ariommus* and *S. cervinus* were consistently resolved as taxa embedded within *Moxostoma*, questioning the monophyly of both *Moxostoma* and *Scartomyzon* if the latter genus is recognized as a distinct taxon. Harris & Mayden (2001) noted that while additional taxa of *Scartomyzon* and *Moxostoma* were needed to expand these data sets and further elucidate the composition of, and limits to, both genera, it was clear the genealogical affinities of *S. ariommus* and *S. cervinus* were within *Moxostoma* and that neither *Scartomyzon* nor *Moxostoma s. l.* were monophyletic groups. Based on this analysis, Harris & Mayden (2001) proposed limiting the Moxostomatini to *Moxostoma* and 'Scartomyzon'; Thoburniini (Hubbs, 1930) was resurrected and expanded to include *Thoburnia* and *Hypentelium*; *Minytrema* and *Erimyzon* were *incertae sedis* within Catostominae (Fig. 2).

In the present study, the phylogenetic relationships among species of *Moxostoma* and 'Scartomyzon' were examined employing mtDNA cytochrome *b* gene sequences. Based on the phylogeny resulting from analysis of these gene

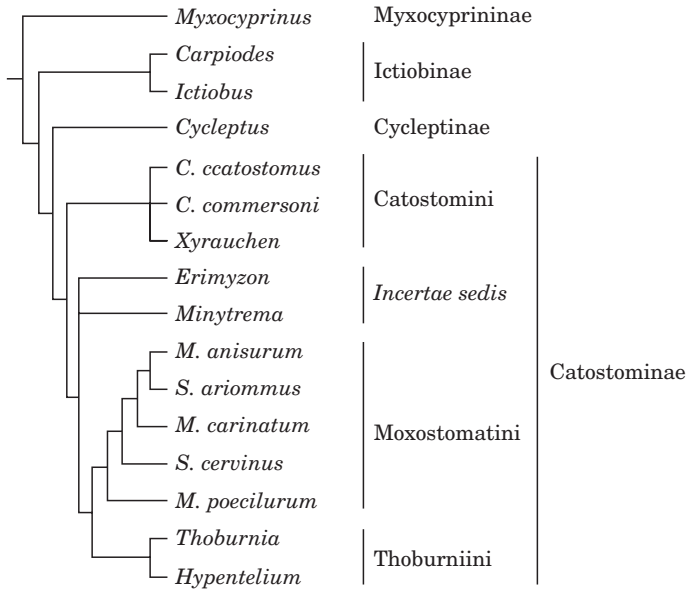


FIG. 2. Classification of the Catostomidae proposed by Harris & Mayden (2001) based on phylogenetic analysis of mitochondrial SSU and LSU rDNA sequences.

sequences, a revised classification is proposed that better reflects the genealogical affinities among these species based on these gene sequence data.

## MATERIALS AND METHODS

### SPECIMENS EXAMINED

The entire mitochondrial cytochrome *b* gene was sequenced in all species of moxostomatid suckers except *Moxostoma lacerum* Jordan & Brayton (extinct) and *Thoburnia hamiltoni* (Raney & Lachner) (Appendix). Taxa sequenced represent all genera, and for *Moxostoma* all subgenera, within the Moxostomatini. *Myxocyprinus asiaticus* (Bleeker) (GENBANK AF036176; Xiao *et al.*, 2001), *Carpiodes carpio* (Rafinesque) and *Cycleptus elongatus* (Lesueur) were used as outgroups following Harris & Mayden (2001). Additional taxa included as functional outgroups representing the Catostomini (Smith, 1992) were *Catostomus catostomus* (Forster), *Catostomus microps* Rutter, *Catostomus occidentalis* Ayres, *Catostomus rimiculus* Gilbert & Snyder, *Catostomus tahoensis* Gill & Jordan, *Deltistes luxatus* (Cope) and *Xyrauchen texanus* (Abbott).

### DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

The QIAGEN DNeasy™ Tissue Kit (Catalogue No. 69506) was used to extract genomic DNA. The mtDNA cytochrome *b* gene was amplified and sequenced from DNA extractions with primers L14724CYP (5'-GTGACTTGAAAAACCACCGTTG-3'; Schmidt & Gold, 1993), CYTB 446L (5'-TYYTATCNGCAGTMCCTTAYRT-3'; this study), CYTB514L (5'-AACGCAACAYTNACACGRTTCT-3'; this study), CYTB529H (5'-RRAAGTGRAAGGCRAAGAAAYCG-3'; this study), and H15915CYP (5'-CAACGATCTCCGTTTACAAGAC-3'; Schmidt & Gold, 1993). PCR reactions consisted of the following: 0.1–0.5 µg genomic DNA; 5 µl 10 × buffer (0.1 M tris-HCl pH 8.5, 0.015 M MgCl<sub>2</sub>, 0.5 M KCl), 5 µl dNTP mixture (2 mM each of dNTP in 10 mM tris-HCl, pH 7.9), 5 µl of a 10 µM solution of each of two primers, 0.5 µl of *Taq*

polymerase, and ddH<sub>2</sub>O added for a final volume of 50 µl. The amplification profile consisted of 94° C for 40 s, 50–52° C for 60 s, and 72° C for 90 s for 35 cycles. Double stranded PCR products were purified with QIAGEN QIAquick™ PCR Purification Kits (Catalogue No. 28106) and sequenced in both directions on an ABI PRISM® 3100 Genetic Analyzer using ABI PRISM® BigDye™ Terminators v2.0 Cycle Sequencing Kit (Catalogue No. 4390242) following the manufacturer's recommendations.

## SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

All DNA sequences were stored and aligned using BioEdit (Hall, 1999). Pairwise comparisons of all taxa were generated using PAUP\* (Swofford, 1998). Comparisons of absolute number of transitions and transversions for each codon position were plotted against maximum likelihood distances (maximum likelihood model selection is discussed below). Nucleotide variation and substitution patterns, including  $\chi^2$  test of homogeneity of base frequencies across taxa, were examined using PAUP\*.

Phylogenies were estimated by maximum parsimony (MP) and maximum likelihood (ML) analyses using PAUP\* (Swofford, 1998). The heuristic search option (100 random addition replications with tree bisection-reconstruction) was used to generate both MP and ML analyses. Non-parametric bootstrap analyses (Felsenstein, 1985) with 1000 pseudo-replicates and 10 random sequence additions were conducted for the MP analyses. As an additional measure of tree stability, Bremer Decay Indices (Bremer, 1988, 1994) were calculated using TreeRot (Sorenson, 1996). ML bootstrap analysis incorporated 200 pseudo-replicates with the heuristic search option. In both analyses, branches with bootstrap values of  $\leq 50\%$  and branch lengths of one or two steps were collapsed. Relative rates test were conducted with PHYLTEST, vers. 2 (Kumar, 1996).

Modeltest (Posada & Crandall, 1998) was used to estimate the model of DNA substitution most appropriate for this data set under maximum likelihood criteria; the selected model was the general time reversible model with some sites assumed to be invariable and with variable sites assumed to follow a discrete gamma distribution (i.e. GTR+I+d $\Gamma$ ). Maximum likelihood settings were as follows: nucleotide frequencies, A=0.3076, C=0.3111, G=0.1148 and T=0.2666; rate matrix, A-C=0.4299, A-G=20.4980, A-T=0.3201, C-G=0.9762, C-T=6.6756, G-T=1.0000; proportion of invariable sites (I)=0.5193; discrete gamma distribution shape parameter (d $\Gamma$ )=0.9843. The Kishino-Hasegawa (1989) test, as implemented in PAUP\*, was used to compare alternative topologies to the nine most parsimonious trees recovered in the unweighted analysis of the cytochrome *b* sequence data.

## TAXON RANKING AND SPECIES CONCEPTS

The evolutionary species concept (ESC; Simpson, 1961; Wiley, 1981; Wiley & Mayden, 2000) was used as the primary concept for the recognition of evolutionary lineages as species. Given that the ESC has no operational component for the identification of evolutionary lineages, however, the phylogenetic species concept (PSC; Eldridge & Cracraft, 1980; Cracraft, 1983), as modified by McKittrick & Zink (1988) to include the criterion of monophyly and diagnosability of lineages, was employed as the operational concept in the recognition of monophyletic lineages as species. In the application of the PSC there is no distinction between species or subspecies in a polytypic species (Cracraft, 1983; Warren, 1992; Mayden, 1997, 1999). Thus, subspecies have no ontological status under this concept and are not recognized. As a consequence, while the species lists of Mayden *et al.* (1992) and Warren *et al.* (2000) employ the most current taxonomy for moxostomatini species, the three subspecies of *M. macrolepidotum* [*M. m. macrolepidotum*, *M. m. breviceps* (Cope) and *M. m. pisolabrum* Trautman & Martin] listed in Warren *et al.* (2000) and the two subspecies of *Scartomyzon congestus* (Baird & Girard) (*S. c. congestus* and *S. c. albidus*; Robins & Raney, 1957) are treated as species in the present study.

## RESULTS

### COMPOSITIONAL BIAS AND SATURATION

Analysis of the complete mtDNA cytochrome *b* gene (1140 bp) sequences among 50 specimens yielded 496 variable sites, with 432 of these sites being parsimony informative. Of the informative sites, 60 (14.0%) were at the first codon position, 15 (3.4%) were at the second codon position, and 357 (82.6%) were at the third codon position. Nucleotide composition was typical of that found in other actinopterygian fishes (Lydeard & Roe, 1997; unpubl. data). Differences in nucleotide composition among and within species were most evident at the third codon position, which exhibited the anti-G bias as reported in other studies (Meyer, 1993; Lydeard & Roe, 1997).  $\chi^2$  tests for homogeneity of base frequencies across taxa for the first two codon positions failed to detect significant differences among taxa ( $P=1.0$ ); however, codon 3 displayed significant differences in base frequencies among taxa (Codon 3,  $\chi^2=200.98$ , d.f. = 147,  $P=0.01$ ), suggesting this heterogeneity could possibly influence phylogenetic reconstruction. Pairwise comparisons of nucleotide substitutions *v.* GTR+I+ $\Gamma$  genetic distances at the third codon position also suggested potential saturation of transition substitutions (unpubl. data). Relative rates test between outgroup taxa, *Erimyzon*+*Minytrema*+Catostomini and Moxostomatini (Smith, 1992), however, failed to reject rate constancy among these clades ( $P=0.05$ ). Although saturation of nucleotide substitutions can potentially affect phylogenetic analyses (Lydeard & Roe, 1997), MP analysis was limited to equal weighting of nucleotide substitutions at all codon positions because it is difficult to make *a priori* decisions regarding weighting schemes, and such weighting may not be entirely justified (Broughton *et al.*, 2000).

### PHYLOGENETIC ANALYSIS

Maximum parsimony and likelihood analyses recovered two and three basal clades within a monophyletic Catostominae (100% bootstrap support and 18 steps to collapse node), respectively (Figs 3 and 4). MP analysis recovered a clade (61% and 3) of the Catostomini (*Catostomus*, *Deltistes* and *Xyrauchen*; Smith, 1992; 98% and 11) and *Erimyzon* plus *Minytrema* (97% and 13); relationships of these clades were unresolved in the ML analysis. Collapsing the Catostomini and *Erimyzon* plus *Minytrema* clade on the MP tree into a trichotomy with the *Moxostoma*, *Scartomyzon*, *Hypentelium* and *Thoburnia* clade resulted in a tree of 2661 steps, 19 steps longer than the most parsimonious trees; the two topologies were significantly different ( $P<0.01$ ). *Erimyzon* was always recovered as monophyletic (100% and 26); *Erimyzon oblongus* (Mitchill) was sister to *Erimyzon tenuis* (Agassiz) plus *Erimyzon succetta* (Lacepède) (94% and 8). *Catostomus* was never supported as monophyletic relative to *Deltistes* and *Xyrauchen* within the Catostomini. *Deltistes* was always recovered as sister to *C. rimiculus* (100% and 17); *C. occidentalis* was basal to these taxa (100% and 20). *Catostoms microps* plus *C. tahoensis* were always recovered as sister taxa (100% and 29).

Both MP and ML analyses recovered a clade containing *Thoburnia*, *Hypentelium*, *Moxostoma* and *Scartomyzon* (80 and 92% and 8) that corresponds with Smith's (1992) *Moxostoma* group (excepting *Erimyzon* and *Minytrema*).

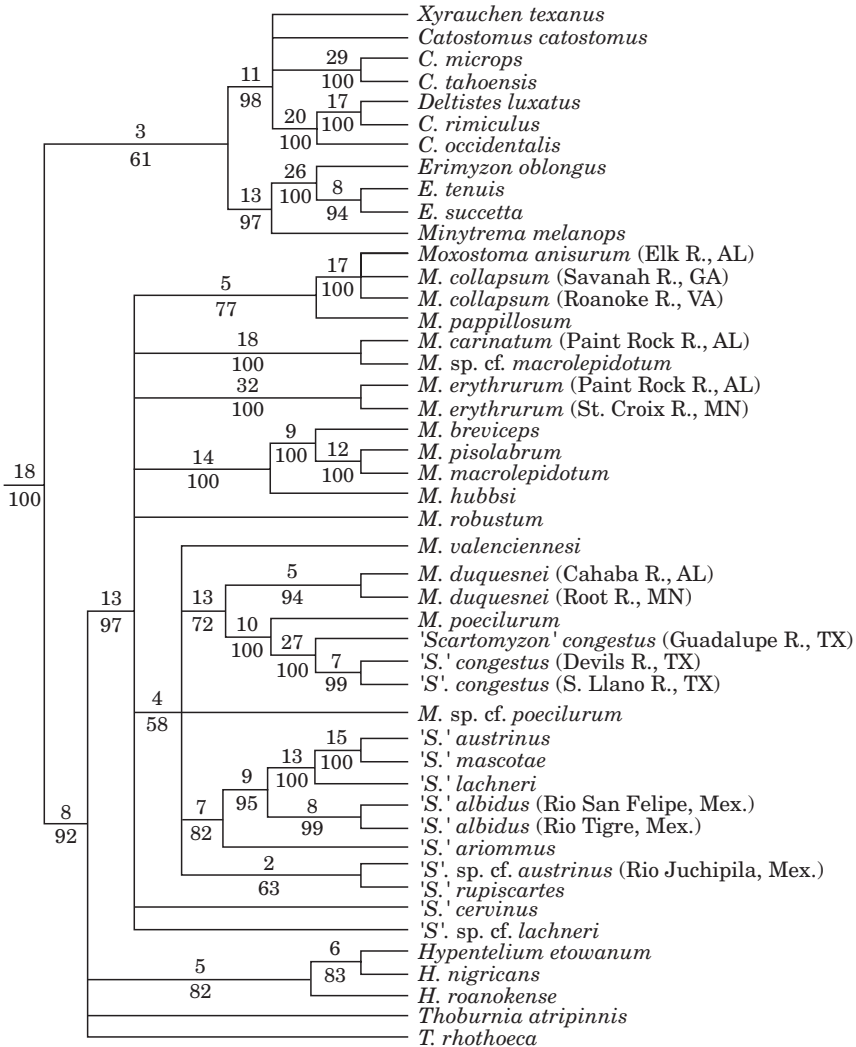


FIG. 3. Phylogenetic relationships of Catostominae based on maximum parsimony analysis of the complete mtDNA cytochrome *b* gene. Topology depicted is the strict consensus of nine equally parsimonious trees of 2642 steps (CI=0.280, RI=0.590, RC=0.165). Numbers above the branches are Bremer decay values; numbers below the branches are bootstrap values based on 1000 replications.

Relationships among these taxa were consistent in both analyses (Figs 3 and 4). MP analysis recovered a polytomy consisting of an unresolved *Thoburnia*, a monophyletic *Hypentelium* (82% and 5), and a clade of *Moxostoma* plus *Scartomyzon* (97% and 13). ML analysis yielded a polyphyletic *Thoburnia*, with *Thoburnia rorthoeca* (Thoburn) as the basal-most taxon in the clade containing *Thoburnia atripinnis* (Bailey), *Hypentelium*, *Moxostoma* and *Scartomyzon*. *Thoburnia atripinnis* was sister to *Hypentelium* (67%); the *T. atripinnis* plus *Hypentelium* clade was sister to a poorly supported *Moxostoma* and *Scartomyzon* clade (63%). *Hypentelium* was monophyletic (77 and 82% and 5) in both MP and ML analyses; *Hypentelium roanokense* Raney & Lachner was sister to

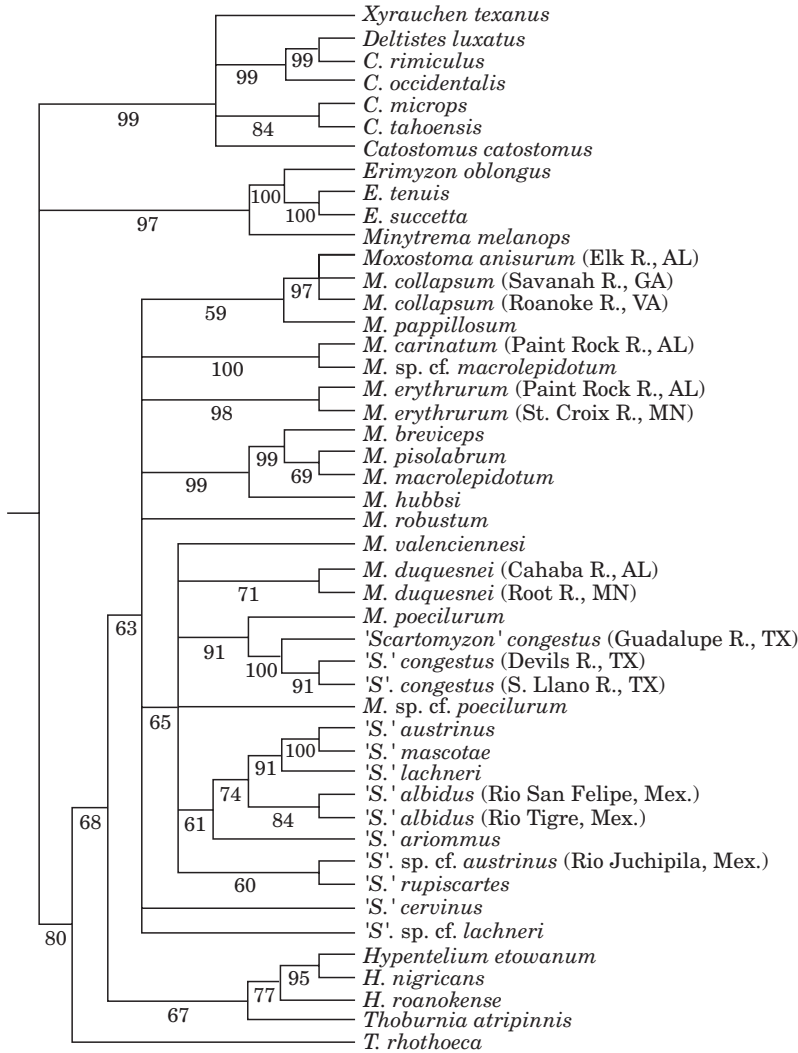


FIG. 4. Phylogenetic relationships of Catostominae based on maximum likelihood analysis (see text for model parameters) of the complete mtDNA cytochrome *b* gene. Numbers below the branches are bootstrap values based on 1000 replications.

*Hypentelium nigricans* (Lesueur) plus *Hypentelium etowanum* (Jordan) (83 and 95% and 6). Constraining *Thoburnia* to be monophyletic under parsimony analysis resulted in nine trees of 2643 steps, one step longer than the nine most parsimonious trees recovered in the unweighted analysis; no significant differences were found among the topologies of these trees with topologies recovered in the unweighted analysis ( $P>0.84$ ).

*Moxostoma* and *Scartomyzon* were resolved as a monophyletic clade (hereafter referred to as the *Moxostoma* clade), although support in the ML analysis was poor (63%) compared to the MP analysis (97% and 13). *Scartomyzon* was never found to be monophyletic, but was recovered as a polyphyletic group always embedded within *Moxostoma*, rendering this genus paraphyletic if

'*Scartomyzon*' continues to be recognized. Relationships recovered within the *Moxostoma* clade were consistent in both analyses, except for the genealogical affinities of *M. duquesnei*. Species relationships within this clade were generally unresolved, although several species groups were recovered in both analyses. *Moxostoma pappillosum* was sister (59 and 77% and 5) to a trichotomy containing *M. anisurum* and two specimens of *M. collapsum* (97 and 100% and 17). *Moxostoma hubbsi* was sister (99 and 100% and 14) to a monophyletic *M. macrolepidotum* species group (99 and 100% and 9); within this species group *M. breviceps* was sister to *M. pisolabrum* plus *M. macrolepidotum* (69 and 100% and 12). *Moxostoma carinatum* from the Paint Rock River, Alabama was sister to *M. sp. cf. macrolepidotum* 'Sicklefin redhorse' (100% and 18). Four species of *Moxostoma* were recovered in a clade of '*Scartomyzon*' species. Constraining *Moxostoma s. s.* to be monophyletic resulted in two trees of 2676 steps, 34 steps longer than the nine most parsimonious trees; these two trees were significantly different ( $P < 0.0005$ ) from the topologies recovered in the unweighted analysis.

'*Scartomyzon*' was recovered as polyphyletic in all nine most parsimonious trees; neither '*S.*' sp. cf. *lachneri* and '*S.*' *cervinus* were recovered with other species of '*Scartomyzon*'. Remaining species of '*Scartomyzon*' were part of a weakly supported polytomy (59 and 65% and 3) that also contained four species of *Moxostoma*: relationships of *M. valenciennesi* and *M. sp. cf. poecilurum* were unresolved; *M. duquesnei* was either unresolved (ML) or sister (MP; 72% and 13) to a clade containing *M. poecilurum* plus '*S.*' *congestus* from Texas (91 and 100% and 10). '*Scartomyzon*' *rupiscartes* (Jordan & Jenkins), from the southeastern U.S.A., was sister to '*S.*' sp. cf. *austrinus* (Rio Juchipila) from the Atlantic slope of Mexico (60 and 63% and 2). '*Scartomyzon*' *ariommus* was the basal-most taxon within a clade of '*Scartomyzon*' species (61 and 82 and 7). '*Scartomyzon*' *albidus* (Girard) (84 and 99% and 8) was sister to a clade (74 and 95% and 9) containing '*Scartomyzon*' *lachneri* (Robins & Raney) sister (100% and 13) to '*S.*' *austrinus* plus '*S.*' *mascotae* (100% and 15). Constraining all '*Scartomyzon*' taxa to be monophyletic resulted in four trees of 2677 steps, 35 steps longer than the nine most parsimonious trees; these four trees were significantly different ( $P < 0.005$ ) from the topologies recovered in the unweighted analysis.

## DISCUSSION

Phylogenetic analysis of the mtDNA cytochrome *b* sequence data yielded a well supported Catostominae, within which were either two or three clades: Catostomini (Smith, 1992) plus *Erimyzon* and *Minytrema* (MP); *Erimyzon* plus *Minytrema* (ML); and, Moxostomatini (minus *Erimyzon* plus *Minytrema*; Smith, 1992). A monophyletic Catostomini is consistent with Smith's (1992) analysis; however, *Catostomus* was never recovered as monophyletic relative to *Xyrauchen* and *Deltistes*. This result may be due, in part, to limited taxon sampling within *Catostomus*. The sister species relationship of *C. rimiculus* plus *D. luxatus* is somewhat problematic, and may be due to either uncertain taxonomic affinities or hybridization. Both *D. luxatus* and *C. rimiculus* are found in the Klamath Lake Basin of southern Oregon and northern California, U.S.A., along with *Chasmistes brevirostris* Cope and *Catostomus snyderi* Gilbert. *Deltistes luxatus*

was originally described as *Chasmistes luxatus* (Cope); Seale (1896) erected *Deltistes* based on the deltoid shaped gill rakers. Bailey *et al.* (1960) transferred this taxon to *Catostomus*. Diagnostic characters for *Deltistes* were subsequently provided by Smith (1975) and Miller & Smith (1981), and Smith's (1992) phylogeny placed *Deltistes* sister to *Chasmistes* in a clade reciprocally monophyletic with *Catostomus*. Recent genetic work on the four species of catostomids from the Klamath Lake Basin based on mitochondrial and nuclear genes suggests that hybridization and introgression may account for the observed parphyly of *Catostomus* (Smith & Dowling, 2001).

Placement of *Erimyzon* plus *Minytrema* as sister to the Catostomini in the MP analysis is inconsistent with Miller's (1959) pre-Hennigian hypothesis and Ferris & Whitt's (1978) phylogeny of 30 species of catostomids based on the loss of duplicate gene expression in isozymes; both hypotheses had *Erimyzon* plus *Minytrema* sister to the Catostomini plus Moxostomatini. This placement is also inconsistent with Smith's (1992) phylogeny, in which *Erimyzon* plus *Minytrema* was sister to the *Moxostoma* group. Twenty-six nucleotide characters support the placement of the clade *Erimyzon* plus *Minytrema* sister to the Catostomini; however, only one character is unambiguous (position 959, a second codon position transition) in support of this relationship. As noted above, collapsing the Catostomini and *Erimyzon* plus *Minytrema* clade yielded a topology significantly different from that of the nine most parsimonious trees. Constraining *Erimyzon* plus *Minytrema* to be consistent with Miller's (1959) and Smith's (1992) hypotheses yielded trees of 2647 and 2650 steps, respectively (five and eight steps longer). Topologies generated by both hypotheses, however, were not significantly different ( $P > 0.06$ ) from the topologies of the unweighted parsimony analysis. Thus, while there is minimal support in the cytochrome *b* data set for the potential sister-group relationship between the Catostomini and *Erimyzon* plus *Minytrema*, the hypotheses of Miller (1959) and Smith (1992) are also consistent with topologies recovered by this data set. As such, while recognition of *Erimyzon* plus *Minytrema* as the tribe Erimyzonini (Hubbs, 1930) is consistent with this data set, phylogenetic affinities of the Erimyzonini within the Catostominae should be considered unresolved until clarified with additional molecular and morphological data. Until these relationships are better elucidated, the Erimyzonini are identified as *incertae sedis* within Catostominae, similar to Harris & Mayden (2001).

*Thoburnia* was recovered as either unresolved (MP) or polyphyletic (ML). Jenkins (1970) noted that interspecific differences in *Thoburnia* were more obvious than intergeneric differences with other moxostomatins; he listed 21 characters distinguishing *T. rhothoeca* and *T. hamiltoni* from *T. atripinnis*. Smith (1992) found no apomorphic characters for *Thoburnia*, although he listed 16 'unique and unambiguous' characters and their character states supporting a monophyletic *Thoburnia*. His relationships within *Thoburnia* were similar to Jenkins (1970). No unambiguous nucleotide characters support a sister group relationship between *T. rhothoeca* and *T. atripinnis*; however, there is one nucleotide character (position 721, a first position transversion) supporting *T. atripinnis* plus *Hypentelium*. Constraining *Thoburnia* to be monophyletic yielded nine trees that were one step longer (2643 steps); these trees were not significantly different ( $P > 0.85$ ) from the topologies recovered in the unweighted analysis.

TABLE I. Classification of the Catostominae based on mtDNA cytochrome *b* gene sequences

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Subfamily Catostominae	
Tribe Catostomini	
Genus	' <i>Catostomus</i> ' (North America and Siberia)
Genus	<i>Xyrauchen</i> (western North America)
Genus	<i>Chasmistes</i> ? (western North America)
Genus	<i>Deltistes</i> ? (western North America)
Tribe Erimyzonini (Hubbs, 1930) <i>incertae sedis</i>	
Genus	<i>Erimyzon</i> (eastern North America)
Genus	<i>Minytrema</i> (eastern North America)
Tribe Thoburniini (Hubbs, 1930)	
Genus	' <i>Thoburnia</i> ' (eastern North America)
Genus	<i>Hypentelium</i> (eastern North America)
Tribe Moxostomatini	
Genus	<i>Moxostoma</i> * (eastern and central North America, south to Mexico)
	(' <i>Scartomyzon</i> ' equals junior synonym of <i>Moxostoma</i> )

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\*For a list of species and correct spelling of names see Appendix.

Constraining *Thoburnia* to be monophyletic and sister to a monophyletic *Hypentelium* also yielded nine trees of 2643 steps; these trees also were not significantly different ( $P > 0.84$ ) from the topologies recovered in the unweighted analysis. Thus, while the mtDNA cytochrome *b* sequence data does not provide direct evidence supporting the monophyly of *Thoburnia*, they are consistent with previous studies supporting both the monophyly of this genus and its sister group relationship with *Hypentelium* (Nelson, 1948; Jenkins, 1970; Buth, 1979a; Smith, 1992; Harris & Mayden, 2001). As such, these taxa are provisionally retained in the tribe Thoburniini (Table I), as suggested by Harris & Mayden (2001). Relationships within *Hypentelium* agree with Jenkins (1970) and Buth (1980), but differ from Smith (1992) in that *H. roanokense* (Atlantic slope) is sister to *H. nigricans* (Mississippi River Basin) plus *H. etowanum* (Mobile River Basin).

Phylogenetic relationships among species of *Moxostoma* and '*Scartomyzon*' were resolved as a polytomy; neither *Moxostoma* nor '*Scartomyzon*', as currently recognized, were monophyletic. Although several currently conceived species groups (e.g. *M. macrolepidotum*) and species (e.g. *M. duquesnei* and *M. erythrurum*) were recovered as monophyletic, one species ('*S. congestus*') and three undescribed forms previously aligned with species were not recovered as monophyletic assemblages.

As currently conceived, *Moxostoma* was recovered as a polyphyletic group; *M. valenciennesi*, *M. duquesnei*, *M. poecilurum* and *M. sp. cf. poecilurum* were recovered in a polytomy with a clade of '*Scartomyzon*' species. *Moxostoma valenciennesi* has not been previously allied with '*Scartomyzon*'. Jenkins (1970), however, noted that his *M. poecilurum* species group (*M. poecilurum* and *M. sp. cf. poecilurum*), which was not monophyletic in this study, shared two features (well-developed body stripes and white lower caudal rays) with most '*Scartomyzon*', but not with other *Moxostoma*. In addition, he noted that 'southeastern populations or subpopulations' (primarily from the Mobile

Basin, Alabama) of *M. duquesnei* shared with 'Scartomyzon' well-developed body stripes (v. absent or poorly developed in other *M. duquesnei*) and a lower dorsal-fin ray count (12 v. 13 in other populations). Samples of *M. duquesnei* from Minnesota and Alabama formed a monophyletic clade in this study; thus, the molecular evidence indicates that *M. duquesnei sensu lato* has phylogenetic affinities with evolutionary lineages within the 'Scartomyzon' clade.

*Megapharynx* (Legendre, 1942) was erected as a monotypic genus for *M. hubbsi*. Robins & Raney (1956) reduced *Megapharynx* in rank to a subgenus of *Moxostoma* and placed *M. valenciennesi* in this subgenus based on the convex margin of the dorsal fin, reddish fin colouration, a black spot at the base of each scale, and high scale counts. Robins & Raney (1956) and Jenkins (1970) noted a historic tendency to associate *M. hubbsi* with *M. carinatum* based on their robust pharyngeal arch and teeth morphology. In contrast, *M. valenciennesi* has a 'light' pharyngeal arch and compressed teeth, similar to other *Moxostoma* (Jenkins, 1970). In this study, *Megapharynx* was never recovered as monophyletic. *Moxostoma hubbsi* was sister to the *M. macrolepidotum* species group; *M. valenciennesi* was resolved with evolutionary lineages within the 'Scartomyzon' clade. In addition, *M. carinatum* was never sister to *M. erythrurum*, as hypothesized by Jenkins (1970) and Smith (1992). Thus, the robust pharyngeal arch character noted above would appear to be autapomorphic in *M. hubbsi* and *M. carinatum*.

Remaining species of *Moxostoma* were recovered as part of the more inclusive *Moxostoma* clade polytomy. Among these taxa were four highly supported species or species groups: (1) *M. pappillosum* plus *M. anisurum* and *M. collapsum*; (2) *M. carinatum* plus *M. sp. cf. macrolepidotum*; (3) a monophyletic *M. erythrurum*; and (4) *M. hubbsi* plus the *M. macrolepidotum* species group. Jenkins (1970) noted that *M. anisurum* and *M. pappillosum* were unique within *Moxostoma* because of their V-shaped lower lips; however, neither Jenkins, based on morphology, nor Buth (1978), based on allozymes, considered the two species to be 'intimately' related. In contrast, the molecular data recovered a relationship between *M. pappillosum* and *M. anisurum* plus *M. collapsum*, concordant with Smith (1992), suggesting the V-shaped lip morphology is a synapomorphy for these species. The two specimens of *M. collapsum*, both from the Atlantic slope of the eastern U.S.A., were recovered as part of a trichotomy with *M. anisurum*. Jenkins (1970) and Buth (1978) regarded *M. collapsum* as a 'race' of *M. anisurum*; subsequently, Jenkins (Rhode, 1998) stated his intention to elevate *M. collapsum*. These molecular data were unable to resolve genealogical affinities among specimens of *M. collapsum* and *M. anisurum*. As such, *M. collapsum* is retained as a species until additional evidence on genetic, morphological and life history variation warrants or precludes its synonymization with *M. anisurum*.

Relationships among members of the *M. macrolepidotum* species group were highly supported (100%); however, relationships of this clade with other *Moxostoma* were unresolved. This observation is consistent with Jenkins' (1970) pre-Hennigian analysis, which did not identify a potential sister species for *M. macrolepidotum*, but is inconsistent with Buth's (1979b) evaluation of this group with *M. carinatum* sister to *M. macrolepidotum*, and Smith (1992), who recovered *M. macrolepidotum* in a clade containing *M. duquesnei*, *M. poecilurum* and

*M. lacerum* (= *Lagochila lacera*). Within the *M. macrolepidotum* species group, *M. breviceps* was sister to *Moxostoma pisolabrum* Trautman & Martin plus *M. macrolepidotum*. Although Jenkins (1970) listed several characters diagnosing *M. breviceps* from *M. pisolabrum* and *M. macrolepidotum*, Jenkins (Rhode, 1998) has only recently stated his intention to elevate *M. breviceps* to specific status. Similarly, Jenkins (1970) noted that the unique 'knob-like' swelling of the upper lip in *M. pisolabrum* was diagnostic for this species, but potential introgression among populations of *M. pisolabrum* and *M. macrolepidotum* in areas of syntopy has resulted in *M. pisolabrum* being retained as a subspecies of *M. macrolepidotum* in recent literature (Warren *et al.*, 2000). No autapomorphic nucleotide characters diagnose *M. pisolabrum* or *M. macrolepidotum* in the cytochrome *b* sequence data; in contrast, three autapomorphic nucleotide characters diagnose *M. breviceps* (positions 511, 572 and 886). Based solely on lack of cytochrome *b* sequence variation between *M. pisolabrum* and *M. macrolepidotum*, application of the PSC (with its criterion of monophyly and diagnosability of lineages) would warrant the subsumption of *M. pisolabrum* into *M. macrolepidotum*. The upper-lip knob character found in *M. pisolabrum*, however, is unique among catostomids (Jenkins, 1970). Jenkins (1970) noted the high degree of separation between *M. pisolabrum* and *M. macrolepidotum* with indices based on this character. Resolution of the taxonomic status of *M. pisolabrum* awaits a more in-depth, population-level examination of genetic variation in this taxon and *M. macrolepidotum*. Further, *M. macrolepidotum* was originally recognized as a central Atlantic slope species closely related to northern and Mississippi River basin populations called *M. aureolum* (synonymized with *M. macrolepidotum* by Hubbs & Lagler, 1958). The specimen of *M. macrolepidotum* examined in this study was collected in the Elkhorn River, Nebraska; no representative of Atlantic slope *M. macrolepidotum* was examined. Thus, the composition of, and limits to, *M. macrolepidotum* awaits inclusion of specimens from the Atlantic slope of North America.

Phylogenetic analysis of the cytochrome *b* sequence data also yielded a polyphyletic 'Scartomyzon'. Constraining all 'Scartomyzon' taxa to be monophyletic yielded four trees of 2677 steps (35 steps longer than the most parsimonious trees); these four topologies were significantly different ( $P < 0.05$ ) from the topologies recovered in the unweighted MP analysis. Thus, while bootstrap support was weak (58 and 65%) for the 'Scartomyzon' plus some *Moxostoma*-species clade in both the MP and ML analyses, there is statistical support for the polyphyly of 'Scartomyzon': phylogenetic relationships of 'S.' *cervinus* and 'S.' sp. cf. *lachneri* may be with species of *Moxostoma*, rather than other 'Scartomyzon'; bootstrap (99%) and Bremer Decay (10 steps) values were high for the *M. poecilurum* plus 'S.' *congestus* clade. Specimens of 'S.' *congestus* and 'S.' *albidus* (originally described as *M. c. congestum* and *M. c. albidum*) were recovered as polyphyletic. This is consistent with Buth's (1978) analysis of allozyme variation in *Moxostoma* (Scartomyzon); *M. c. congestum* was sister to *M. cervinum* and *M. lachneri*, while *M. c. albidum* was paraphyletic and sister to *M. austrinum* and *M. mascotae*. Thus, molecular data, in conjunction with Buth's (1978) allozyme data set, provide support for the recognition of 'S.' *albidus* as a distinct species.

Genealogical affinities within the ‘*Scartomyzon*’ clade were generally inconsistent with hypotheses advanced by [Robins & Raney \(1956, 1957\)](#), [Buth \(1978\)](#) and [Smith \(1992\)](#); however, their hypotheses of a biogeographic pattern between the south-eastern U.S.A. and Mexico was recovered, albeit with different species pairs. ‘*Scartomyzon*’ sp. cf. *austrinus* (Rio Juchipila, Mexico) was sister to ‘*S.*’ *rupiscartes* (south-eastern U.S.A.); however, support for this branch was weak (60 and 63% and 2); there were no unambiguous apomorphies for this clade. As such, the hypothesized sister species relationship between these taxa are considered tentative.

Phylogenetic relationships among remaining ‘*Scartomyzon*’ taxa, however, were highly supported by the molecular analyses, with branches possessing 82–100% bootstrap support values in the MP analysis (61–100% in ML) and requiring seven–15 steps to collapse. ‘*Scartomyzon*’ *ariommus* was the basal-most member of this clade; this is consistent with [Buth’s \(1978\)](#) hypothesis, but inconsistent with those of [Jenkins \(1970\)](#) and [Smith \(1992\)](#), wherein ‘*S.*’ *ariommus* was more closely related to *Thoburnia* and *Hypentelium* than ‘*Scartomyzon*’. [Robins & Raney’s \(1956\)](#) *M. robustum* species group (‘*S.*’ sp. cf. *lacherni*, ‘*S.*’ *congestus*, ‘*S.*’ *austrinus* and ‘*S.*’ *mascotae*) was polyphyletic; ‘*S.*’ sp. cf. *lacherni* does not appear to have any close genealogical affinities with the other species in the group, while ‘*S.*’ *lachneri* (not originally included in this species group) is sister to ‘*S.*’ *austrinus* plus ‘*S.*’ *mascotae*. These relationships are consistent with [Buth \(1978\)](#) and [Smith \(1992\)](#), although either ‘*S.*’ *cervinus* or ‘*S.*’ sp. cf. *lachneri*, respectively, were also included in this clade in their analyses. As far as is known, no other aquatic taxa display such a pattern of east–west disjunction between sister taxa as that exhibited by ‘*Scartomyzon*’. [Robins & Raney \(1957\)](#) suggested that species distributions within ‘*Scartomyzon*’ are remnants of a once continuous ancestral distribution. Given that the major preglacial drainages in the central and eastern U.S.A. flowed from north to south ([Mayden, 1988](#)), there does not appear to be a logical paleohydrological mechanism that would explain the current distribution of sister taxa within the clade of ‘*Scartomyzon*’ species at this time. Thus, [Robins & Raney’s \(1957\)](#) suggestion may be the most plausible hypothesis to account for the perplexing biogeographic patterns exhibited by ‘*Scartomyzon*’.

Based on the phylogenetic relationships resolved in this study ([Figs 2 and 3](#)), a revised classification of the subfamily Catostominae is proposed ([Table I](#)). This classification modifies that proposed by [Harris & Mayden \(2001\)](#) by recognizing the tribe Erimyzonini ([Hubbs, 1930](#)), subsuming ‘*Scartomyzon*’ into *Moxostoma*, and restricting the tribe Moxostomatini to *Moxostoma*. In this classification, the listing convention of [Nelson \(1972, 1974\)](#) is employed. Potentially para- or polyphyletic groups are noted in shutter quotes; groups that may not warrant recognition, or those that have uncertain placement, are followed by a ‘?’

Although this study has advanced the knowledge of some generic and species-level relationships in the redhorse and jumprock suckers, there are clearly several issues pertaining to relationships among the evolutionary lineages identified herein, and their concomitant biogeographic patterns, that require further elucidation. The disjunct distribution of sister taxa within the ‘jumprock suckers’ needs clarification, as well as the identification of a potential

paleohydrologic mechanism possibly responsible for their distributions if these relationships are corroborated using other data. Further, phylogenetic relationships among, and taxonomic composition of, evolutionary lineages identified for some species of *Moxostoma* and allied genera (e.g. *Thoburnia*) require further study. This is especially important given the endangered or threatened conservation status of several species within *Moxostoma*.

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APPENDIX. Taxa analysed, museum voucher number, GENBANK accession number and sampling locality of specimens. UAIC, University of Alabama Ichthyological Collection; OS, Oregon State University Ichthyological Collection; JFBM, James Ford Bell Museum, University of Minnesota; RC-REJ, Roanoke College, Robert E. Jenkins Field Number

Taxon	Voucher No.	GenBank Accession No.	Sampling locality
<b>Outgroup</b>			
<i>Carpiodes carpio</i>	UAIC 11219.08	AF454867	Honey Creek, Richardson County, Nebraska, U.S.A.
<i>Cycleptus elongatus</i>	UAIC 11371.01	AF454868	Big Sunflower River, Big Sunflower County, Mississippi, U.S.A.
<i>Myxocyprinus asiaticus</i>		AF036176	Xiao <i>et al.</i> (2001)
<b>Functional Outgroup</b>			
<i>Catostomus catostomus</i>	UAIC 11237.04	AF454871	Belt Creek, Cascade County, Missouri, U.S.A.
<i>Catostomus microps</i>	OS 12122BB	AF454872	Johnson Creek, Modoc County, California, U.S.A.
<i>Catostomus occidentalis</i>	OS 11196BB	AF454873	American River, El Dorado County, California, U.S.A.
<i>Catostomus riniculus</i>	OS 15908	AF454875	Lower Klamath River, Klamath County, Oregon, U.S.A.
<i>Catostomus tahoensis</i>	OS 11221BB	AF454874	Eagle Lake, Lassen County, California, U.S.A.
<i>Delistes luxatus</i>	OS 15922	AF454870	Williamson River, Klamath County, Oregon, U.S.A.
<i>Xyrauchen texanus</i>		AF454869	Fin clip from Dr D. Buth, University of California at Los Angeles, U.S.A.
<b>Ingroup</b>			
<i>Erimyzon oblongus</i>	UAIC 11109.09	AF454876	Mill Branch Creek, Colbert County, Alabama, U.S.A.
<i>Erimyzon succetta</i>	UAIC 12286.01	AF454878	Hatchet Creek, Alachua County, Florida, U.S.A.
<i>Erimyzon tenuis</i>	UAIC 12730.04	AF454877	Cedar Creek, Mobile County, Alabama, U.S.A.
<i>Hypentelium etowanum</i>	UAIC 12523.08	AF454908	Conasauga River, Polk County, Tennessee, U.S.A.
<i>Hypentelium nigricans</i>	UAIC 11138.02	AF454909	Bear Creek, Marion County, Alabama, U.S.A.
<i>Hypentelium roanokense</i>	UAIC 13449.02	AF454910	North Fork Roanoke River, Roanoke County, Virginia, U.S.A.
<i>Moxostoma albidum</i>	UAIC 13446.01	AF454902	Rio El Tigre, Tamaulipas, Mexico
<i>Moxostoma albidum</i>	UAIC 12365.01	AF454901	Rio San Felipe, Tamaulipas, Mexico
<i>Moxostoma anisurum</i>	UAIC 11606.02	AF454880	Elk River, Limestone County, Alabama, U.S.A.
<i>Moxostoma ariommmum</i>	UAIC 12071.01	AF454903	South Fork Roanoke River, Montgomery County, Virginia, U.S.A.
<i>Moxostoma austrinum</i>	UAIC 12375.01	AF454898	Arroyo Ahuacapan, Jalisco, Mexico
<i>Moxostoma breviceps</i>	UAIC 11314.08	AF454888	Duck River, Bedford County, Tennessee, U.S.A.
<i>Moxostoma carinatum</i>	UAIC 11005.03	AF454883	Paint Rock River, Marshall County, Alabama, U.S.A.

## APPENDIX Continued

Taxon	Voucher No.	GenBank Accession No.	Sampling locality
<i>Moxostoma cervinum</i>	UAIC 11004.01	AF454906	Craig Creek, Craig County, Virginia, U.S.A.
<i>Moxostoma collapsum</i>	UAIC 12376.05	AF454881	Savannah River, Franklin County, Georgia, U.S.A.
<i>Moxostoma collapsum</i>	UAIC 11007.03	AF454882	Roanoke River, Roanoke County, Virginia, U.S.A.
<i>Moxostoma congestum</i>	UAIC 13506.05	AF522290	Guadalupe River at Guadalupe River State Park, Kendall/Comal Counties, Texas, U.S.A.
<i>Moxostoma congestum</i>	UAIC 13508.05	AF522291	Devils River at Devils River State Natural Area, Val Verde County, Texas, U.S.A.
<i>Moxostoma congestum</i>	UAIC 13512.05	AF522292	South Llano River at boat ramp on Texas Road 2169 in Junction, Kimble County, Texas, U.S.A.
<i>Moxostoma duquesnei</i>	UAIC 11310.09	AF454894	Cahaba River, Bibb County, Alabama, U.S.A.
<i>Moxostoma duquesnei</i>	JFBM 38581	AF454895	Root River, Olmsted County, Minnesota, U.S.A.
<i>Moxostoma erythrurum</i>	UAIC 12237.03	AF454886	Rock River, Colbert County, Alabama, U.S.A.
<i>Moxostoma erythrurum</i>	JFBM 37043	AF454887	St Croix River, Pine County, Minnesota, U.S.A.
<i>Moxostoma hubbsi</i>	RC-REJ 1822	AF522289	St Lawrence River at Lavaltrie, Berthier County, Quebec, Canada
<i>Moxostoma lachneri</i>	UAIC 12370.02	AF454900	Mountain Creek, Harris County, Georgia, U.S.A.
<i>Moxostoma</i> sp. cf. <i>lachneri</i>	UAIC 12462.03	AF454907	Fisher Creek, Surry County, North Carolina, U.S.A.
<i>Moxostoma macrolepidotum</i>	UAIC 11221.10	AF454890	Elkhorn River, Antelope County, Nebraska, U.S.A.
<i>Moxostoma</i> sp. cf. <i>macrolepidotum</i>	UAIC 11643.01	AF454885	Little Tennessee River, Macon County, North Carolina, U.S.A.
<i>Moxostoma macotae</i>	UAIC 12374.01	AF454899	Rio de la Pola, Jalisco, Mexico
<i>Moxostoma pappillosum</i>	UAIC 13462.01	AF454883	Black Water River, Franklin County, Virginia, U.S.A.
<i>Moxostoma pisolabrum</i>	UAIC 11154.05	AF454889	Spring River, Jasper County, Missouri, U.S.A.
<i>Moxostoma poecilurum</i>	UAIC 11442.01	AF454896	Tallapoosa River, Tallapoosa County, Alabama, U.S.A.
<i>Moxostoma</i> sp. cf. <i>poecilurum</i>	UAIC 12746.13	AF454897	Halawakee Creek, Lee County, Alabama, U.S.A.
<i>Moxostoma robustum</i>	UAIC 11916.01	AF454891	Pond 9A, Piedmont National Wildlife Refuge, Jones County, Georgia, U.S.A.
<i>Moxostoma rupiscartes</i>	UAIC 12376.06	AF454905	Middle Fork Broad River, Franklin County, Georgia, U.S.A.
<i>Moxostoma valenciennesi</i>	JFBM 36305	AF454893	Mississippi River, Hubbard County, Minnesota, U.S.A.
<i>Thoburnia atripinnis</i>	UAIC 13463.01	AF454911	Unnamed creek on State Highway 839 south of Forkton, Monroe County, Kentucky, U.S.A.
<i>Thoburnia rhothoeca</i>	UAIC 11009.05	AF454912	Catawba Creek, Roanoke County, Virginia, U.S.A.