

CYPRINID FISHES OF THE SUBGENUS CYPRINELLA OF NOTROPIS

FROM SOUTHEAST TEXAS, U.S.A., AND NORTHEAST MEXICO

by

Gladys Lou Lytle

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

ARIZONA STATE UNIVERSITY

June 1972

CYPRINID FISHES OF THE SUBGENUS CYPRINELLA OF NOTROPIS
FROM SOUTHEAST TEXAS, U.S.A., AND NORTHEAST MEXICO

by

Glady Lou Lytle

has been approved

May 1972

APPROVED:

_____ Chairman

Supervisory Committee

ACCEPTED:

_____ Department Chairman
_____ Dean, Graduate College

CYPRINID FISHES OF THE SUBGENUS CYPRINELLA OF NOTROPIS

FROM SOUTHEAST TEXAS, U.S.A., AND NORTHEAST MEXICO

by

Glady Lou Lytle

An Abstract of a Thesis Presented in
Partial Fulfillment of the Requirements
for the Degree
Master of Science

ARIZONA STATE UNIVERSITY

June 1972

ABSTRACT

Four nominal species of the cyprinid fish genus Notropis, subgenus Cyprinella, from southern Texas, U.S.A. and northeastern Mexico, were studied through computer analysis and more classical taxonomic procedures. These fishes are termed the "N. proserpinus group," and are separated from the "lutrensis - ornatus" group of the subgenus as being of earlier origin and relatively unrelated. The "lutrensis - ornatus" group is restricted to N. lutrensis and its derivatives in the U.S.A. and in Mexico, with N. ornatus being considered a distinct lineage. The four nominal forms assigned to the N. proserpinus group are considered as valid species and are redescribed and compared—N. rutilus, N. lepidus, N. xanthicara, and N. proserpinus.

A survey of geologic evidence coupled with the presence of aquatic animals of western affinities in river basins far to the east is used to develop a probable history of the Rio Grande drainage network. This, along with information on the dispersal of other members of the subgenus Cyprinella from a "hub" of differentiation in the Mississippi River system is used to re-construct the origins of the proserpinus group and to delineate their relationships to other member of their subgenus.

change

ACKNOWLEDGEMENTS

This ~~was prepared~~ *was prepared* ~~is, itself, an acknowledgment~~ *of the requirements*
~~of a M. S. degree in Zoology~~ *degree in Zoology* ~~the senior advisor~~ *the senior advisor* ~~directed~~ *directed*
~~by~~ *by* ~~my graduate committee~~ *my graduate committee*, D. I. Rasmussen and M. A. Cazier;

their assistance untiring, their encouragement timely and galvanic.

Grateful thanks are extended to my ~~many~~ *colleagues* fellow graduate students who offered welcome succor in moments of need.

Special appreciation is extended to the Taximetrics Laboratory (D. J. Rogers, G. Esterbrook, et al.), University of Colorado, Boulder, who provided valuable advice and encouragement, who processed parts of ~~the~~ data. Thanks are also due the curators of museums for loan of specimens, given later. The research was supported largely by N.S.F Grant No. GB-6477-X, to W. L. Minckley.

I strove to complete this work for my family, Lytles and Sylves- believed in me when least I believed in myself.

TABLE OF CONTENTS

INTRODUCTION1
METHODS AND MATERIALS3
RESULTS	8
<u>Taximetry by Levels</u>	... 8
<u>Taximetry by CalComp Analysis</u>	...12
<u>Discussion of Taximetrics Analyses</u>	14
<u>Descriptive Taxonomic Analyses</u>	22
ACCOUNTS OF SPECIES	29
<u>Notropis xanthicara</u> Minckley and Lytle	29
<u>Notropis lepidus</u> (Girard)	32
<u>Notropis proserpinus</u> (Girard)	34
<u>Notropis rutilus</u> (Girard) ..	36
<u>Descriptive Comparisons</u>	38
ORIGINS AND AFFINITIES	47
<u>Geologic background</u>	47
<u>Faunal Evidences for an Integrated, Disrupted, and Re-connected</u> <u>Rio Grande system</u>	51
LITERATURE CITED	59
APPENDIX A. Characters and designated character states	67
APPENDIX B. Provenance of materials utilized ..	72

LIST OF TABLES

Table 1. Summary of linkages occurring among sub-clusters depicted in Figure 1 at level 14 of the Taxometrics analysis by levels, expressed as percentages of the over-all totals of intra- and interconnectedness of each sub-cluster; total numbers of linkages for each sub-cluster are given in parentheses ...17

Table 2. Summary of linkages occurring among sub-clusters depicted in Figure 1 at level 14 of the Taxometrics analysis by levels; expressed as percentages of the over-all totals of intra- and interconnectedness of each sub-cluster, but excluding 'problem' collections 36, 48, and 54; numbers of linkages for each subcluster are given in parentheses--see text for further explanation 19

Table 3. Means and ranges (in parentheses) for 14 morphometric features of four nominal forms of the N. proserpinus group of the genus Notropis, subgenus Cyprinella. Data are given as thousandths of standard length used as whole numbers 40

Table 4. Percentages of total specimens examined for four nominal forms of the N. proserpinus group of the genus Notropis, subgenus Cyprinella, having numbers of meristic characters listed toward the left 41

LIST OF FIGURES

Figure 1. Cluster graphs showing serial clustering of the forms of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*, through 14 levels of progressively lower values of similarity 9

Figure 2. Sky-line plot showing along its y-axis the values of similarity and along its x-axis the samples of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*, in the order in which they were first taken into a cluster--see text for further explanation 13

Figure 3. Mature specimens of *Notropis xanthicara* (paratypes; ASU 3728) from Rio Garabatal, 6.7 km south and 8.8 km west of Cuatro Ciénegas, Coahuila, Mexico, 16 August 1968. Upper is a 36 mm SL female, lower is a 42 mm SL, tuberculate male..... 30

Figure 4. Distribution of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*; dots represent localities for specimens examined, open circles are for literature or museum records, and x marks the general location of the Cuatro Ciénegas basin, given as an insert map 31

Figure 5. Mature specimens of *Notropis lepidus* (TU 22263) from headsprings at waterfall, Nueces River, Real County, Texas, 25 July 1954. Upper is a 41 mm SL female, lower is a 55 mm SL, tuberculate male..... 33

Figure 6. Mature specimens of *Notropis proserpinus* (ASU 1701) from the Devil's River at Baker's Crossing, Val Verde County, Texas, 11-12 April 1965. Upper is a 44 mm SL female lower is a 54 mm SL, tuberculate male 35

Figure 7. Mature specimens of *Notropis rutilus* (UNL 616) from unnamed creek 2.5 km southwest El Ranchito, Nuevo Leon, Mexico. Upper is a 37 mm SL female, lower is a 39 mm SL, tuberculate male..... 37

INTRODUCTION

Holden and Stahlaker (1970), studying a species complex within the cyprinid fish genus *Gila*, demonstrated the versatility in taxonomic ichthyology of the taximetric computer technique developed by Estabrook (1966), and later refined and tested by Estabrook and Rogers (1966) and Wirth, et al. (1966). This program analyses, according to character states, objects which are involved in a hierarchy. These objects may be individual organisms, or collections of specimens, depending upon the circumstances. Wirth, et al. (1966) expanded mathematical structures within the program to include biological descriptions of more non-quantitative natures, such as color patterns or colors themselves if ranked into character states, and thereby allowed an investigator's professional judgements to be incorporated into the program context. This was an invaluable aid in bridging the gap between rigorous demands of computer formats on one hand and interpretation of non-quantitative features of an organism on the other.

The complex of fishes here subjected to taximetric and more conventional taxonomic analyses has been referred to the "lutrensis ornatus group," subgenus Cyprinella, of the speciose genus Notropis (Gibbs, 1957a). The red shiner, Notropis iucensis (Baird and Girard) and a group of nominal forms now synonymized with it or otherwise closely associated is presently under study by Salvador Contreras Balderos, Universidad de Nuevo Leon, Mexico. The work of Contreras Balderos and A. J. ... have been invaluable in final interpretations. The four nominal

species studied, ~~by~~ _____ (= Notropis lepida Girard (1856), Moniana (= Notropis) proserpina Girard (1856), Moniana (= N.) rutila Girard (1856), and Notropis xanthicara Minckley and Lytle (1969), have been variously treated relative to N. lutrensis throughout their taxonomic history, but are here considered distinct from that species (or complex) on the bases of common breeding colors of the nuptial males (yellowing of the fins and green or aqua-marine coloration of the body), features of male nuptial tuberculation, similar ecological relationships among themselves and relative to N. lutrensis (when sympatric with them), and a rather intimate, although allopatric for the most part, distributional pattern. They are found in the lower Rio Grande (= Rio Bravo del Norte) and associated drainages, southern Texas, U. S. A. and northeastern M'xico (principally in the states of Coahuila and Nuevo Leon. A fifth species, yet to be described from the Rio Conchos, Chihuahua, Mexico, was placed with the last four as near relative by Minckley and Lytle (1969), but is now thought to represent an independent derivative from the N. lutrensis line, perhaps near Notropis garmani Jordan (1885) (= N. lutrensis garmani) of the Rio Nazas system, Mexico (Contreras B., and W. L. Minckley, unpublished). Codoma (= Notropis?) ornata Girard (1856) should be removed from the subgenus Cyprinella on the bases of reproductive behavior, breeding coloration, and morphology (Minckley, ~~ms.~~ ^{unpublished}).

METHODS AND MATERIALS

The ~~taximetrics~~ computer program involves clustering **techniques** whereby aggregates of objects (collection means, in ~~the~~ study) are built through association of each object with its nearest, most similar, neighbor. ~~Pair-wise~~ Pair-wise comparisons are made. ~~This is to say~~ after all available descriptive information about each object has been entered, paired comparisons are made between objects. One object with its definitive array of character states is compared with another object's array, and a value is provided which indicates the degree of similarity of descriptive information between the objects. This is the similarity value, c . When two objects are compared and the c value is assigned, a cluster is formed. Within the program, all possible comparisons between objects are made. When two members, each in a separate aggregation, link ~~to each other~~, the two respective aggregations are ultimately considered as one. In this manner, by making comparisons between and among objects within and outside a cluster, a **heirarchy** of linkages is generated. Note that clusters may be designated by their similarity values, e.g., an "0.73-cluster," or, in more general usage, as a "c-cluster."

The numerical value for isolation of any given **c-cluster** is termed the "moat." This is derived by subtracting from any given value the next largest similarity value for a pair of objects, one object from within the cluster and the object outside. The moat measures the external discontinuity, or empty space, surrounding a cluster. If a moat is large, closest objects to the cluster

should not be readily confused with cluster members. If ~~it is~~ small, however, non-members might be relatively similar to members, and thereby cause confusion.

In summary, structuring into partitions and internal connections form levels may be viewed as a continuum from initial, distinct objects, clustering together hierarchically through all allowable partitions, and terminating in a single cluster. Each level may be meaningful, singly, with ~~formation~~ formation of clusters that warrant formal recognition at some taxonomic level.

Intermediate forms also are defined as those which link or share properties with two or more, otherwise isolated clusters; these may or may not be of taxonomic significance. Within the taximetrics design, an intermediate form is defined as an object which, when removed from the data, results in formation of two or more clusters from an original, larger cluster (Wirth, et al., 1966). persistence of an articulation point (= intermediate object) through a long range of linking-similarity-values indicates the clusters it connects are otherwise isolated from one another.

A total of 971 specimens was studied from 60 different localities from throughout most of the range of this complex. From 1 to 30 individual specimens from each collection were examined in detail, depending upon numbers and sizes of fish in the collection. No fish shorter than 30 mm standard length (SL) was used due to incomplete development of characters in smaller individuals. The largest fish measured was 60 mm SL. All counts were made under appropriate magnification, and measurements were made with dividing calipers to the

nearest tenth mm on a steel rule and converted to thousandths of SL prior to analysis. ^{as whole} Fifty-four characteristics were studied, and of these 14 were morphometric, 5 were meristft, and 35 were qualitative (Appendix A). Counts, and all measurements excepting prepelvic length (~~from tip~~ of snout to insertion of pelvic fin), width of body (greatest width at midline directly above pelvic fin insertions) postdorsal length (dorsal fin origin to end ^{of} hypural plate; Gibbs, 1957b), and postpelvic length (pelvic fin insertion to end ^{of} hypural plate), were made following Hubbs and Lagler (1964). Two other measurements, from origin of dorsal fin to origin of anal fin (Koehn and Minckley, 1965) and from origin of dorsal fin to nape, were not described by Hubbs and Lagler. Qualitative data principally concerned melanophore and nuptial tubercle distributions and sizes over the body and fins (Appendix A). A listing of specimens ~~examined may be~~ ^{is} found in Appendix B, listed by river systems and segments. All data were obtained from preserved material made available by curators of fishes at the following institutions: Arizona State University, Collection of Fishes, Tempe (ASU); University of Kansas, Museum of Natural History, Lawrence (KU); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); ^{de Avila} Universidad de Nuevo Leon, Laboratorio de Vertebrados, Monterrey (UNL); Texas Natural History Collectfon, Austin. (TNHC); and Tulane University Collections, New Orleans (TU). Notes on breeding -oloration of males and ecology of the various species were extracted from the literature or were provided by W. L. Minckley and others from Arizona State University, University of Texas, and University of Michigan.

Because of the u te volume of data, it was decided to treat them per collection rather than specimen by specimen. Means of the morphometric and meristic characters were calculated, however, because of the basically non-numerical nature of qualitative characters, were obliged to assign values and then utilize modes rather than means. A mode was taken as the trend demonstrated by a character within a col-lection, and obviously entailed a judgement on my part. Codification and the multipartitioning of data, requisite for the computer analyses, was as follows: 1) each collection was assigned a number, from 1 through 60, and each character was also assigned a number, from 1 through 54; 2) each character was, in turn, partitioned into from 2 through 5 character states each (Appendix A); and 3) morphometric characters had five character states each, the 5 meristic and 35 qualitative characters were assigned from 2 to 4 states each. Choice of the character was one any number of states per character is possible, depending upon the capacity of available computers.

Generation of character states is a somewhat mechanical process. In Instances they were determined by plotting the mean or mode of each character of all collections into a histogram. The histogram was then partit:--ed into five, ural groupings of means, using the morphometric data as an example. As such, the histogram was treated as a in the manner of a bell-shaped distribution. Since there were 60 collections, and a near-normal distribution pattern was desired, the groupings consisted of 5, 10, 30, 10, and 5 collection means per group. The two groupings with 5 means representing

extremes in the range, the 10 groups of 10 means being less extreme, and the 30 means in the central range representing the greatest concentration of means for that character--each character state (1 - 5) was delimited by its own range of means. Head length, for example, which had an over-all range of means from 246 to 292 thousandths SL, was ultimately partitioned into five shorter ranges: 1) 246 - 253; 2) 254 - 260; 3) 261 - 275; 4) 276 - 284; and 5) 285 - 292. These shorter ranges (= partitions) were the character states used as input for that feature. Meristic features were much more tightly arrayed than were morphometric data, and had fewer points for segmentation. Consequently, they were broken into from 2 to 4 partitions/or character states/each. Qualitative data were highly variable, but also were transformed into histogram arrangements and extensive variation was compacted into usable schemes. The resulting partitioning was ordinally arranged for each character studied no ranking of characters was involved as none of the states ^{are} between features hierarchical. At completion, each collection was defined by its total array of 54 charac , Jr. state numbers and each state pertained to only one of the 54 characters studied. These data were ~~in the first 4 columns of IBM data~~ cards sent to the Taximetrics Laboratory, University of Colorado, for processing. Returned printouts of the cluster program computed on a CDC-6400 and a generated skyline plot, by CalComp Plotter were fundamental aids to ~~see~~ this study. Subsequent to receipt of the computer-generated data on implied relationships between collections, "classical" or "intuitive" taxonomic work was required to determine reasons for unexplained and unanticipated variances in ~~the~~

over-all pattern of variations, an decision economic
population.

RESULTS

Taximetry by Levels

The results of taximetric analyses by levels are clarified and more easily understood by concurrent reference to text and to Figure 1. At level 1, the first cluster began forming with a linkage between collections 3 and 7, both from the Cuatro Ciénegas basin, Coahuila, Mexico. At this level, $c = .81481$, which is to say that 81.48% of the two collections' attributes used as input to the computer, were similar.

At level 2, $c = .79630$, a second cluster, distinct from and totally unconnected to the first, formed between collections 45 and 46, both from the Nueces River system, Texas. At level 3, $c = .77778$, a third core formed between collections 19, 20, and 21, from the Rio Salado de los Nadadores, Coahuila, and all from sites with a few kilometers of each other. The two other cluster cores added no new members, nor were any connections indicated between clusters that had formed.

At level 4, $c = .75926$, a fourth cluster-core formed through linkage of collections 57 and 58, both from the Pecos River system, Texas. At this level the first-formed cluster added another sample from the Cuatro Ciénegas basin, whereas the other two cores remained unchanged.

From levels 4 through 11 ($c = .75926 - .62963$, respectively) the first formed core added all samples (1 - 14) from the Cuatro Ciénegas

Figure 1. Cluster graphs showing serial clustering of the forms of the N. proserpinus group of the genus Notropis, subgenus Cyprin-
ella, through 14 levels of progressively lower values of similarity

basin, and formed no extra-cluster connections. This occurred progressively, without sub-cluster formation. The second-formed core behaved similarly after its origin at level 2, but finally consolidated by enveloping a small subcluster (samples 40 and 43), which formed at level 9 and persisted through level 10. The third-formed cluster-core behaved quite differently, developing into two sub-clusters at level 7, then 3 at level 8, and not consolidating until connections were made with the fourth-formed cluster at level 10 (Fig. 1). The fourth core behaved similarly to the second-formed cluster in having a small sub-cluster (collections 55 and 59), which formed at level 6, and be incorporated into the main core at level 7.

At level 9, the geographic congruence of the four lines of cores (including the yet-attached sub-cores of the second-formed lineage) was examined. All collections involved in the first core were from the Cuatro Ciénegas basin, as mentioned before, and could be identified as Notropis xanthicara. The second core to form (including its small sub-core of collections 40 and 43) included only material from the Nueces River system, Texas, and could be considered as N. lepidus. The third-forming core(s) included samples from the Rio Salado system, northeastern Mexico, only, and could be tentatively assigned to N. rutilus. The last cluster, with one exception, included only samples from within the known range of N. proserpinus, generally the Pecos and Devil's rivers of Texas.

At level 10, $c = .64815$, two small sub-clusters formed adjacent to the rutilus-like cluster, and the four collections involved were

one (number 31) from the southernmost tributary of the Rio Salado system, plus three (33, 34, and 39) from the Rio San Juan system of Nuevo Leon, Mexico. Another collection from the Rio San Juan system, which appeared as a connectant to the proserpinus cluster through collection 57 (Pecos River system) in level 9, extended its connection at level 10 to collection 59, also of the Pecos system. Other connections formed between the rutilus-like cluster and proserpinus, between collections 21 and 22 (rutilus, Rio Salado) and collections 55 (Devil's River) and 57 (Pecos River system).

At level 11, $c = .62963$, the rutilus-like and proserpinus clusters remained relatively distinct (excepting collection 36, see later), and expanded their sub-clusters by connecting with more free members, formerly outside (including the small sub-clusters present at level 10, and others), plus increasing their internal connectedness.

At level 12, $c = .61111$, two major linkage phenomena occurred. A connection formed between collections 3 (xanthicara) and 16 (rutilus). The latter collected by E. G. Marsh, 1939, from near Cuatro Ciénegas, Coahuila. On the bases of verbal confirmation by the collector in 1961 (W. L. Minckley, pers. comm.) and of other fishes and other organisms collected by Marsh, there is no doubt that the fish came from within that basin (Hubbs and Miller, 1965; Miller, 1969; Minckley, 1969; Minckley and Lytle, 1969; Minckley, 1975; Minckley and Lytle, 1969). However, rutilus-like fish no longer occur there (Minckley and Lytle, (1969). The second major linkage occurred among collections 49 (Rio Frio, Texas) and 43 (Nueces River, Texas) of lepidus, and collections 38 (Rio San Juan, Nuevo Leon) and 36 (Rio Pilon, Nuevo Leon) of

rutilus, respectively. This technically resulted in formation of a single, large cluster, including all four nominal forms as four sub-clusters. Level 13, $c = .59259$, is not illustrated (Fig. 1) or specifically discussed here since it added little to the over-all fabric of the analysis. At level 14, $c = .57407$, all collections were taken into the total cluster. The taximetrics program does not allow passage of output below the level where all objects are connected, in this instance level 14. If c-values could be relaxed below level 14, the samples would be expected to become more and more interconnected, and the pattern would be one of increasing catenation.

Taximetry by CalComp Analysis

Prior to discussion of this ~~kind of~~ approach to the data a short explanation of its visual representation, Figure 2, is necessary. Horizontal bars of the graph are simply a linear representation of the connection(s) that has occurred between two or more samples at a particular level of similarity. Similarity values are along the y-axis and the x-axis indicates the sequence in which the 60 collections were first added to a cluster (Fig. 1). Vertical bars represent the moats which exist between samples, the moat being the mathematical difference which separates collections, as described earlier. It must be stressed that development of each of the skylines, from top to bottom, does not indicate which new collection was attached to which other collection in a cluster, but merely that a given level of similarity, the new collection was indeed added. Due to this, Figure 1 is a necessary adjunct to interpretation of the

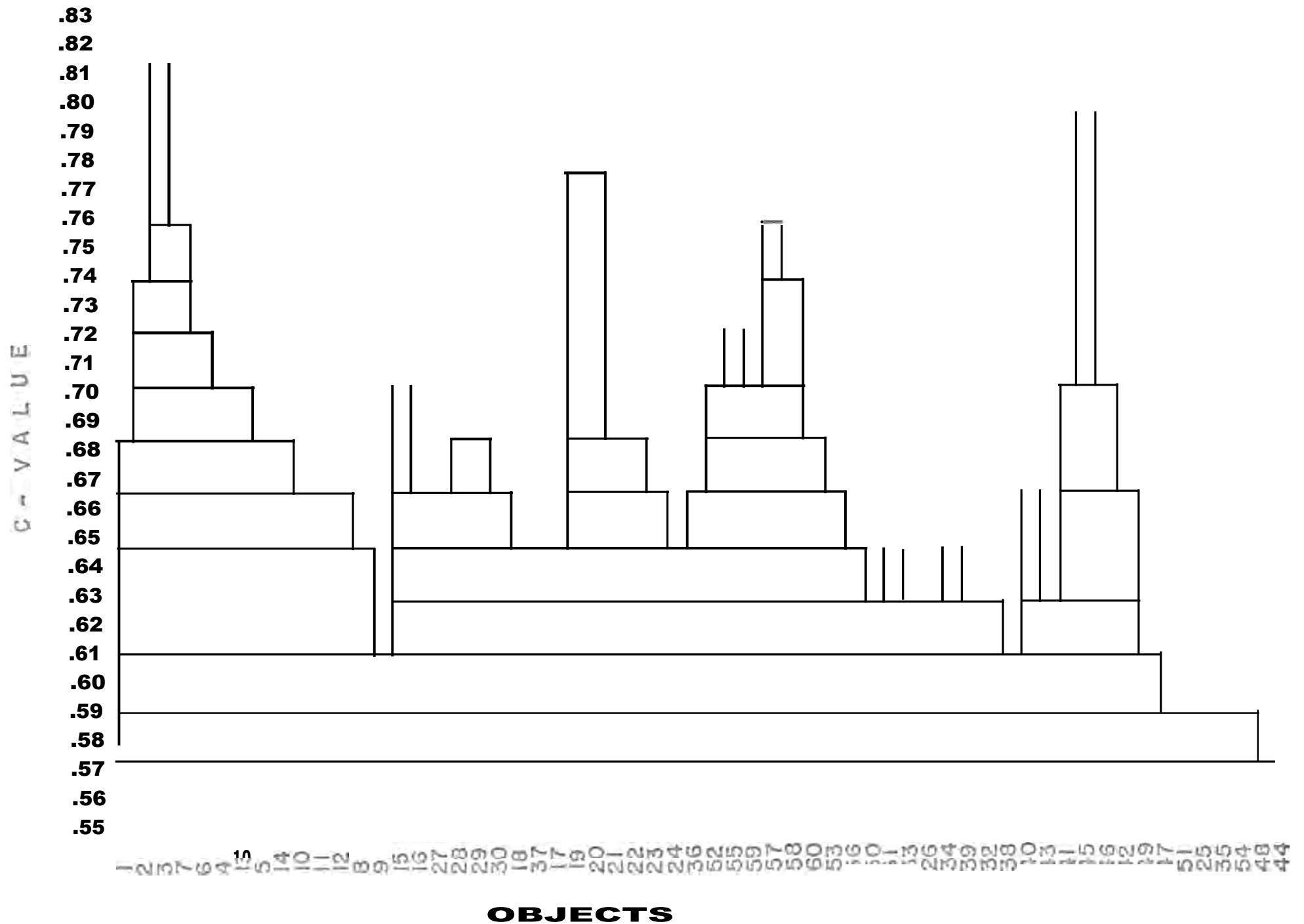


Figure 2. sky-line plot showing along its y-axis the values of similarity and along its x-axis the samples of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*, in the order in which they were first taken into a cluster; see text for further explanation.

skyline plot, since, in the former, the nuances of connections that occur in Figure 2 are specified.

A cursory scan of Figure 2 reveals five evident peaks, the constituents of which are identical to the clusters (or lineages of sub-clusters) shown at level 9 in Figure 2. From left to right the peaks represent N. xanthicara, rutilus (two peaks), proserpinus, and lepidus. Moats indicate not only the separateness within each form, but also that which exists between them, what is not demonstrated, however, is that with each lower similarity value, connections increase within each group, resulting in formation of ever-more-similar groups.

At level 10, $c = .64815$ (Fig. 1), the peaks of the pair of rutilus clusters (or sub-clusters) are connected by a single bar to proserpinus, indicating a similarity of characteristics among the samples represented in the clusters at that time. At level 12, a single horizontal bar crosses all four (or five) peaks, indicating one large cluster containing sub-clusters that are more dissimilar at higher c-values and more similar at lower c-values. Only a few collections are left to be taken into this master cluster, and this was realized at level 14, thus terminating the cluster.

Discussion of Taximetrics Analyses

At level 12 (Fig. 1), N. xanthicara made its first extra-cluster connection with a member of the rutilus complex, and by level 14, only three such connections had occurred, another with a rutilus and one with collection 56, proserpinus from the Devil's River, Texas. At the last level, a total of 110 interconnection had occurred ~~at level 14~~

various collections from the Cuatro Cienegas basin, and the internal distinctiveness of that form seems irrefutable (Table 1). The first outside connection made by xanthicara was with collection 16, one of Marsh's series from the Cuatro Cienegas basin. This tends to support the occurrence of rutilus within that basin when conditions were more propitious for its survival since some hybridization between rutilus and xanthicara after secondary contact through canalization may be indicated. The second connection with rutilus was with collection 20, from the Rio Salado de los Nadadores adjacent to the Cuatro Cienegas basin. Here again, on the basis of "intuitive" taxonomy, ~~myself~~ and others have ~~gotten~~ an impression that some introgressed characteristics from xanthicara are present in upper Rio Salado de los Nadadores rutilus stocks. It is unfortunate that some additional levels of similarity could not have been run to test this possibility. The connection between xanthicara and proserpinus (Fig. 1) may be fortuitous, but, on the other hand, it may be somewhat of a key to the complex pattern of clustering seen in the rutilus complex. In short, ~~I may have weighted~~ ^{MAY HAVE WEIGHED} the analyses inadvertently by ~~s~~ ^{WSE} ongly emphasizing pigmentary characteristics. N. xanthicara is relatively invariable in its pigmentation ~~since~~ ⁱⁿ it inhabits clear headsprings and their outflow waters (Minckley and ~~Wyle~~ ^{WYLE}, 1969); ~~how~~ ^{DECON} ~~ever~~ ^{ATTAIN} other forms may vary widely in expression of melanophore patterns in response to variations in clarity, or temperature, or both, of waters in which they occur (plus a myriad of other factors). This will be discussed more fully below.

Also at level 12, the cluster referable to N. lepidus made its first extra-cluster connection with the rutilus - proserpinus sub-clusters. These involved a Rio Frio sample (49) and a Rio San Juan rutilus (38) and another between a Nueces River lepidus (43) and the enigmatic collection 36, from the San Juan system but otherwise close to proserpinus. The lepidus cluster was strongly homogeneous until level 12, with the western samples, from the east and west Nueces rivers coming together as a group around sample 45 (West Nueces River) and eastern samples converging about sample 46 (Mill Creek, Bandera County, Texas; Rio Frio system). At level 14, the lepidus sub-cluster was not nearly as cohesive as N. xanthicara, maintaining only 64% of its connections internally, and having identical percentages of total connections to proserpinus and the San Juan form of rutilus (Table 1; 18%).

The collections referred to N. proserpinus, excluding collection 36, remained relatively well defined until level 9, and retained considerable integrity throughout all levels of scrutiny dictated by the program. At level 14, however, only 53% of the connections made by samples referred to proserpinus were with others of their kind, and the percentages of connections progressively downstream along the Rio Grande were in file (Table 1), ranging from 26% with Rio Salado collections to 10% in the San Juan, then to 9% for the Nueces.

Cluster:Ag of the diverse group of fishes referred to N. rutilus was obviously the most complex of the four nominal forms. Generally, it occurred as follows: 1) the upper Rio Salado collections fell out as a fairly stable unit; 2) the same holds true for the lower Salado -

Table 1. Summary of linkages occurring among sub-clusters depicted in Figure 1 at level 14 of the taximetrics analysis by levels, expressed as percentages of the over-all totals of intra- and interconnectedness of each sub-cluster; total numbers of linkages for each sub-cluster are given in parentheses.^{1/}

Drainage systems	Devil's and Pecos systems	Rio Salado system	Salado and San Juan systems	Rio San Juan system	Nueces River system	Cuatro Cienegas basin
Devil's and Pecos systems (88)	53	17	18	22	18	1
Rio Salado system (127)	26	65		43	2	2
Salado and San Juan systems (176)			77			
Rio San Juan system (49)	10	17		18	18	0
Nueces River system (44)	9	1	5	18	64	0
Cuatro Cienegas basin (13)						97

^{1/} All values were rounded to the nearest percentage point, hence some do not add to 100% or the vertical plane.

^{2/} Included material from San Felipe Springs, Val Verde County, Texas.

Rio Sabinas de Nuevo Leon samples; 3) these ultimately formed a core united about Marsh's early collections (15 and 16; Fig. 1) from the upper Rio Salado system (Cuatro Ciénegas system); and 4) collections from the Rio San Juan system became attached to the main cluster in a haphazard manner, and subsequent to connection of the rutilus cluster(s) to proserpinus. Despite this complexity, when one considers the over-all connections revealed in level 14 of Figure 1, 77% of the fish referred to rutilus (rios Salado and San Juan combined) were intra-connected, a far greater cohesiveness than shown within proserpinus samples (53%), with extra-cluster connections to proserpinus being about 26% and those with lepidus ca. 5% (Table 1). Within river systems, rutilus-types from the Rio Salado system showed 65% interconnectedness an equivalent connectedness to proserpinus and the San Juan rutilus (17% each; Table 1). But the San Juan collections showed only 18% interconnectedness, 18% to lepidus, and a similar amount, 22%, to proserpinus, but tended very strongly, 43%, toward collections from the Rio Salado. When three collections, to be discussed immediately below, are excluded from calculations of intra- and ~~extra-connectedness~~ (Table 2), the relationships just discussed are far more evident, but the pattern of relations between collections from the various river systems and nominal forms remain essentially unchanged.

One of these last "problem" samples, sample 36 from El Ranchito, near Matamorelos, Nuevo Leon, in the Rio San Juan, should geographically be considered rutilus; however, its first connection, at level 9 (Fig. 1) was with sample 57 (proserpinus), and at level 10, it gained a

Table 2. Summary of linkages occurring among sub-clusters depicted in Figure 1 at level 14 of the taxonomic analysis by levels; expressed as percentages of the over-all totals of intra- and interconnectedness of each sub-cluster, but excluding "problem" collections 36, 48, and 54; numbers of linkages for each sub-cluster are given in parentheses--see text for further explanation.^{1/}

Drainage	Devil's and Pecos systems	Río Salado system	Salado and San Juan system	Río San Juan system	Nueces River system	Cuatro Ciénegas basin
Devil's and Pecos systems (75)	61	17	14	5	13	1
Río Salado system (124)	26	65	--	43	2	2
Salado and San Juan systems (161)			81			----
Río San Juan system (37)	3	15	----	27	13	0
Nueces River system (38)	5	0		16	74	0
Cuatro Ciénegas basin (113)	0	1		0	0	97

1/ See footnotes, Table 1

connection with sample 59, another proserpinus. Both these collections are from the Pecos River system, Texas, the most geographically distant samples available within the over-all matrix. At level 11, it connected with sample 55, still proserpinus, and finally with sample 27 from the Rio Sabinas de Coahuila, at Musquiz. From levels 12 through 14, the sample gained many connections within proserpinus (7), and directly (2) plus indirectly (through proserpinus samples with samples of rutilus) established itself as a link not only between proserpinus and rutilus, but also between proserpinus and lepidus (3 direct linkages). The two additional samples, 48 from the Rio Frio near Knippa, Uvalde County, Texas, and 54 from the Devil's River east of Del Rio, Texas, emerged from the matrix very late (level 13), indicating that they were quite different from all other samples, and like sample 36 formed connections that were not geographically congruent. Sample 48, geographically a lepidus, made its primary connection with sample 26 from the Rio Salado near Monclova, Coahuila, and at level 14 made its only other connection with sample 60, a proserpinus from Independence Creek, Texas. Sample 54, geographically a proserpinus formed its initial connection at level 13 with sample 43 of lepidus from the Nueces River near Uvalde, Texas, and at level 14 formed linkages between itself and samples 42 (upstream East Nueces River, Texas), 49 (upstream Rio Frio, Texas), and 59 (Howard Creek, Pecos River system, Texas), lepidus, lepidus, and proserpinus, respectively.

In summary of the taximetrics results, and generally excluding the last three samples discussed from consideration at this time, at

level 10, the nominal N. rutilus (samples 21 - 22, Rio Salado de los Nadadores) formed connections with two samples of N. proserpinus (55 and 57, Devil's River, Texas. At level 11, there were seven rutilus-proserpinus connections; at level 12, 13 such connections occurred, and at level 14, 25 such connections are evident (excluding sample 36 which, if included, increases the number of linkages at level 14 to 32). The rutilus - proserpinus connections are first made between core-cluster members, and subsequently between peripheral cluster members, and this is a direct indication of the similarities between the two nominal forms. Therefore, rutilus is most similar to proserpinus, followed by lepidus and xanthicara, with the last being most distinctive of the four (Fig. 1; Tables 1-2). The last three forms emanate from the rutilus core in a spoke-like fashion, with lepidus far nearer proserpinus through rutilus than is xanthicara.

On the basis of a definition given by Wirth, et al. (1966) and Esterbrook (1966) for an intermediate form, I could also designate rutilus as intermediate between xanthicara and lepidus, since no explicit connections between the last two are demonstrated. However, study of Figure 1, level 14, shows a linear connection from sample 3 of xanthicara to sample 16 of rutilus, which, in turn, connects to another rutilus (sample 38). and thence to collection 49 of lepidus. Lower levels of similarity doubtless would result in direct connections between xanthicara and lepidus, which would reduce the value of rutilus as an intermediate between them. The limitation of the taximetrics program to cease out at the time all objects are clustered was unfortunate in since internal connectedness and external

linkages would have been valuable in final interpretation of ~~the~~ data.

Descriptive Taxonomic Analyses

More ~~classical~~ analyses of the fishes concerned here convinced Vit, as alluded to before, that inadvertent weighting of data, or blocks of data, strongly influenced ~~the~~ computer output. This hinged mostly on the use of variable characters, or features of sexual or seasonal occurrence. In the fishes studied, ~~melanophore~~ distribution and expression provided a graded scale which could be almost as easily influenced by extraneous environmental factors as by genetic factors, nuptial ~~tubercle~~ distributions and sizes are obviously a function of sexual condition of the fish at the time of preservation (Koehn, 1965, and references cited), fin sizes and shapes also vary with the sexual state of individual specimens, and states of preservation, not to mention the time factor in fading of coloration and basic patterns of pigmentation under conditions of preservation, all may have come into play. Despite these factors of variability in qualitative features of this species groups, decisions were based principally on color patterns and nuptial tubercle distributions and relative sizes over the heads, bodies, and fins. Specimens were carefully examined, and re-examined visually, plus a ~~graphic technique~~ only briefly mentioned by Wirth, et al. (1966) was used to bring the mass of data together and review it for descriptive comparisons of the various population samples. The graph, which is not ~~presented~~ here, was a segmental arrangement with the x-axis being the characters broken to their

respective character states, with 2 to 5 squares allotted to each, depending on its number of states. The y-axis represented the 60 collections. Each collection was then described on the graph by darkening of the square for the appropriate character state. In this way, certain features were immediately identified as useless, or at least weak, by their chaotic arrangement of character states within blocks of collections, and others could be defined as useful, in the sense that they demonstrated differences between population samples. The 'problem' samples also were re-examined prior to final conclusions, as were a number of samples of the species group from northern México which had become available since termination of the formal study. Visual comparisons of many features discussed may be made by reference to Figures 3, and 5 - 7, plus Tables 3 and 4

At the onset, it must be stated that about 17 of the 35 qualitative characters used in the computer input seem questionably variable, which tends to reduce the percentage of linkage values in Tables 1 and 2 considerably, at least 10% and perhaps as much as 15%. Secondly, the possibilities of hybridization influencing morphology of some of the populations studied seems quite high, and this will be detailed later. And, thirdly, the use of population means may well have obscured individual variants, or misclassified individuals within some of the samples, thus reducing the value of the computer output even more.

The Cuatro Ciéneqas species, *N. xanthicara*, and the Texas form, *N. lepidus*, as indicated by taximetry and by more classical taxonomic study, are uniformly distinctive fishes, each in its own right and

involving different characteristics. *N. proserpinus* from Texas also is readily identifiable, although existing as locally-differentiated stocks in spring-fed tributaries of the Pecos and Rio Grande. That form now is known to occur in some spring-fed tributaries of the Rio Grande in northern Coahuila, Mexico (Fig. 7). *N. rutilus* shares many features in common with *N. proserpinus*, but far more so among its also-locally-differentiated populations (Tables 1 - 2). The complex pattern of clustering of *rutilus* stocks (Fig. 1) may provide some clue to the relatively high level of linkage with *N. proserpinus* (Tables 1 - 2). As mentioned earlier, visual examination of certain collections by myself and others seem to indicate that some gene flow may be occurring (or in the past, may have occurred) from *N. xanthicara*, downstream in the Rio Salado de los Nadadores, and thence throughout much of the Rio Salado system, into *N. rutilus*. The dark pigmentation patterns of *xanthicara* (Fig. 3), through selective introgression, might well tend to cause linkage of the Salado forms of *rutilus* more closely to *proserpinus* (a more darkly pigmented form) than to *lepidus* (generally more lightly pigmented). This interpretation is weakened by the general cohesiveness of *rutilus* within the Rio Salado system and the haphazard manner in which samples from the Rio San Juan became associated with the primordial sub-clusters of *rutilus* at level 11 and below (Fig. 1). It is strengthened on the other hand by the presence of Marsh's early collections, which serve to bring the divergent forms of *rutilus* together in the final analysis. Primary connections among *rutilus* and *proserpinus*, and subsequently between *rutilus* and *xanthicara* do, however, involve population samples from the Rio Salado

system.

An additional factor, which may have been missed by me and may, in fact, be very difficult to resolve, is the possibility of some hybridization between at least *N. proserpinus* and/or *N. rutilus* with local forms of *N. lutrensis*. The coastal form of the last species, *N. l. suavis* (Girard), occurs east of the Nueces River system of Texas (Hubbs, 1954), and except for its breeding colors in the nuptial male (reddened fins and blue body) is quite similar to *N. lepidus*; *N. lepidus* and *N. l. luxiloides* (Girard) (= *suavis*; Hubbs, 1954) are known to hybridize in the Guadalupe River system, Texas (Hubbs, 1951, 1954; Hubbs, et al., 1953). I examined no material from the Guadalupe River system, and *N. lutrensis*, to my knowledge, does not occur in the upper Nueces system. *N. l. lutrensis*, the Plains form of that minnow, is broadly sympatric with *N. proserpinus* in the Devil's and Pecos River systems (Hubbs, 1958), and with *N. rutilus* in both the Rio Salado and San Juan systems (Val Guerra, 1952; Hubbs and Hubbs, 1958; Contreras B., 1967 and pers. comm.). In almost all instances, *lutrensis* is the more-downstream form, in more turbid, warmer waters, while *rutilus* or *proserpinus* tends to occur just downstream from head-spring situations. Excluding the breeding colors of mature males, hybrids between any of these forms (especially *proserpinus* and *rutilus* where nuptial coloration is quite similar) would be quite difficult to detect; to my knowledge, none of these hybrid combinations has been reported from nature. Laboratory produced hybrids between *N. lepidus* and *N. proserpinus*, however, showed marked abnormalities in certain segmental features, with anal fin-ray counts, for example, greatly

exceeding the means for either of the parental stocks (Hubbs, 1956). Unfortunately, no such hybridization studies have been performed among other fishes within this species group.

The three problem collections, 36, 48, and 54, were somewhat unsatisfactorily categorized by critical, visual examination. Collection 36, the more difficult of the three was strongly linked to *N. proserpinus* by the computer analyses (Fig. 1, levels 9 - 14), but according to its geographic occurrence should have been *N. rutilus*. Included in the sample are some highly-tuberculate, darkly-pigmented fish referable to *rutilus*, with little doubt, plus a number of individuals that may be referred to *N. rutilus* X *N. l. lutrensis*, with some reservations. In this instance it is proposed that the pigmentary and some nuptial tubercle characteristics caused the convergent placement of the series with *proserpinus*. Collections 48 (geographically *lepidus*, but linked initially to *proserpinus*) and 54 (geographically *proserpinus* but linked to *lepidus*), are comprised of relatively small, faded specimens, and also are referred to their geographic, rather than computer-generated, relatives.

A strong possibility, which should be examined more thoroughly in the future, is that *N. proserpinus* and *N. rutilus* occur sympatrically in the Rio Salado system, as convergent, sibling species, or at some degree of hybridization and interfertility, and that I missed subtle differences that might exist between the forms. The discovery of a population of the former in northern Coahuila, upstream from the Rio Salado, increases the possibility for secondary contact and some form of miscegenation. Essentially complete interfertility between

far more divergent species of the subgenus Cyprinella, *N. v. venustus* (Girard) x *N. lutrensis*, is well documented in some Texas streams that have received human disturbances (Hubbs and Strawn, 1956, and papers cited), and the Rio Salado system has certainly received its share of disturbance in past decades through diversions for irrigation, impoundment, and pollution from steel and associated industries. Here again, the use of means for definition of character states would obviously have suppressed discovery of *uc* phenomena, if they were the case.

If the interpretation, at this level of analyses, is that Rio Salado samples represent intergrades between proserpinus of the Pecos River - Devil's River systems and rutilus of the San Juan basin, two major factors seem to work in its favor. Firstly, the percentages of connectedness (Tables 1 and 2) would seem to indicate this, with the Salado samples at 65% intraconnectedness trending toward proserpinus in interconnectedness of 26%, and the San Juan samples at 18% (a very low percentage, perhaps insignificant, and indicating exceedingly high intra-population variability) trending toward Salado samples at 43% interconnectedness. And, secondly, the primary connection between Rio Salado and Rio San Juan collections is through sample 31, from the Rio Sabinas de Nuevo Leon (Salado system), which is geographically most adjacent to the San Juan system. Operating against such an interpretation is the 65% intraconnectedness of Rio Salado collections and an interconnectedness of only 17% toward the San Juan (with an equal level toward proserpinus), plus the strong cohesiveness, 77% within

Rio Salado - Rio San Juan collections when they are combined (Table 1). If the Rio Salado forms are considered intergrades between proserpinus and rutilus the latter would be relegated to subspecific rank by line priority.

If intergradation is indicated in my data it certainly is of a disorganized nature, with little geographic congruence, and should be studied more carefully for its content of biological information. In arid and semi-arid zones, intergradation or hybridization patterns may well tend to resemble that described here, because of disruption, then re-connection, then repeated sequences of the two in existing drainage systems, not to mention the probable drainage changes that have occurred in the more distant past. Whatever the case, excluding *N. lepidus* and *N. xanthicara* as well differentiated species, I chose to retain the forms *N. proserpinus* and *N. rutilus* as "semi-species" at least, in the sense of recent writings of Mayr (1970). All four kinds are allopatric, with the lack of sympatry between xanthicara and rutilus being enigmatic since causal connections now exist between their respective ranges in the Rio Salado de los Nueces, and neither form occurs within them. *N. lepidus* is restricted to headwaters, presumably by competition with *N. l. saavis*, or some other factor, and the Rio Grande is isolated downstream by sea from both the Nueces and Guadalupe systems. And, *N. proserpinus*, in its obvious avoidance of downstream habitats such as the mainstream Rio Grande (Robinson, 1959), again perhaps as a result of the presence of *N. lutrensis*, is isolated in a manner similar to that which prevents movements of *N. rutilus* into the Rio Grande mainstream.

ACCOUNTS OF SPECIES

Type materials of the fishes studied, with the exception of *N. xanthicara*, were not examined, and I relied heavily on two published works, Hubbs and Ortenberger (1929) and HuLbs (1954), plus segments of an unpublished manuscript by C. L. Hubbs and the late Myron Gordon entitled "Fishes of Northern Mexico," on file at the University of Michigan Museum of Zoology and graciously loaned to W. L. Minckley by R. R. Miller, in sorting out the following synonymies. The divergent and inconsistent "lumping" and "splitting" of Girard's (1856), and ~~others~~ species of fishes now referred to *Notropis*, principally by Jordan and his colleagues (discussed by Gibbs, 1957a), plus the loss of a number of types or type series (or mixing of more than one species within a series of co-types), makes synonymies tentative at best, and broadly over-lapping with those of the difficult *N. lutrensis* complex. I have therefore only listed the references that seem most likely to pertain, totally or in part, to the fishes studied by me, with a minimum of comment as to the reasons for such ~~listing~~ listing by ~~earlier~~ authors.

Notropis xanthicara Minckley and Lytle

Cuatro Cienegas shiner, Fig. 3; insert map, Fig. 4.

Notropis sp., Minckley, 1969: 40.

Notropis xanthicara Minckley and Lytle, 1969: 493 (orig. descr., type material at the University of Michigan Museum of Zoology (holotype UMMZ 188782, plus ~~paratypes~~ paratypes), at Arizona State University (paratypes), and at Universidad de Nuevo Leon (paratypes).

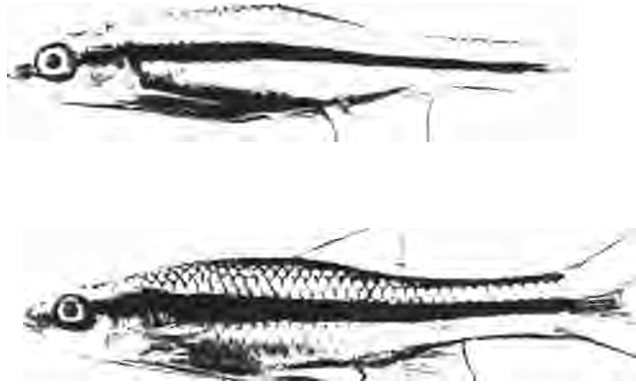


Figure 3. Mature specimens of Notropis xanthicara (paratypes, ASU 3728) from Rio Garabatal, 6.7 km south and 8.8 km west of Cuatro Ciénegas, Coahuila, México, 16 August 1968. Upper is a 36 mm SL female, lower is a 42 mm SL, tuberculate male.

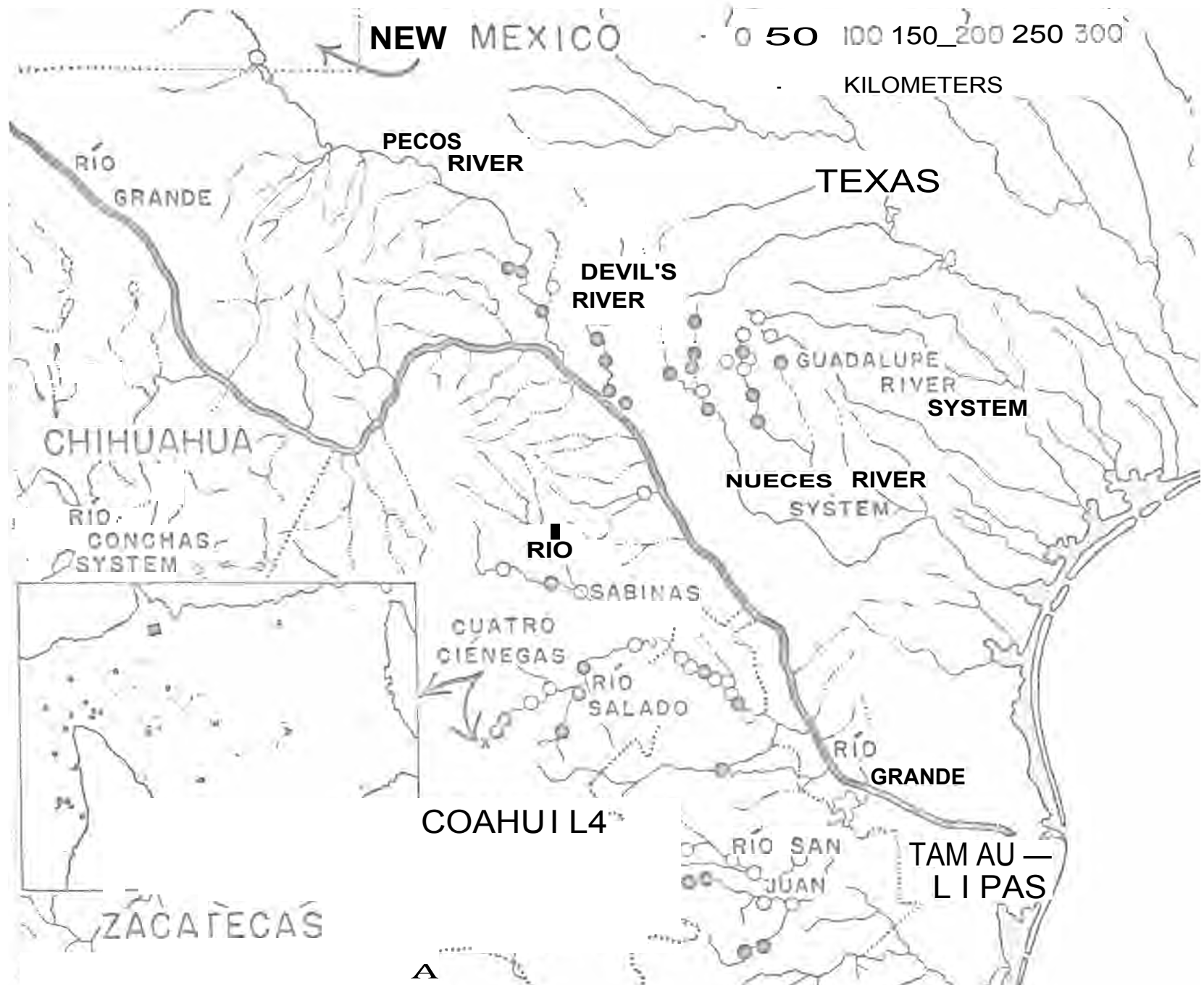


Figure 4. Distribution of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*; Dots represent localities for specimens examined, open circles are for literature or museum records, and x marks the general location of the Cuatro Ciénegas basin, given as an insert map.

Range. --Known only from within the Cuatro Ciénegas basin, central Coahuila, northeastern Mexico.

Notropis lepidus (Girard)

Edwards Plateau shiner, Figs. 4 - 5.

Cyprinella lepi'da, Girard, 1856: 197-198 (orig. descr.; types apparently lost [Hubbs, 1954]; Rio Frio, Texas), 1859a: 268; Jordan, 1878b: 421, 1885: 124.

Moniana frigida, Girard, 1856: 200 (orig. descr.; Rio Frio, Texas); 1859a: 56, 1859b: 276; Jordan, 1885: 125; Jordan and Evermann, 1896: 271; Hubbs and Ortenberger, 1929: 74-75; Jordan, et al., 1930: 131.

Cyprinella frigida, Jordan, 1878b: 421.

Notropis sp., Jordan, 1885: 124.

Notropis frigidus, Jordan and Everman, 1896: 271; Meek, 1903: 771-774, 1904: 75 (mis-ident.); Fowler, 1910: 279; Hubbs and Ortenberger, 1929: 740.

Notropis lutrensis, Jordan and Evermann, 1896: 271-272 (part); Hubbs and Ortenberger, 1929: 74-75 (part); Hubbs, et al., 1953: (part); Eddy, 1957: 118 (part); Moore, 1957: 64 (part); many others.

Notropis bubalinus, Jordan and Evermann, 1896: 273 (part).

Cyprinella bubalina, Jordan, et al., 1930: 130 (part).

Notropis lepidus, Hubbs, 1954: 281, 283, 1956: 463-469, 1957: 98, 1958: 7, Hubbs and Strawn, 1956: 343; Moore, 1968: 83; Minckley and Lytle, 1969: 491.

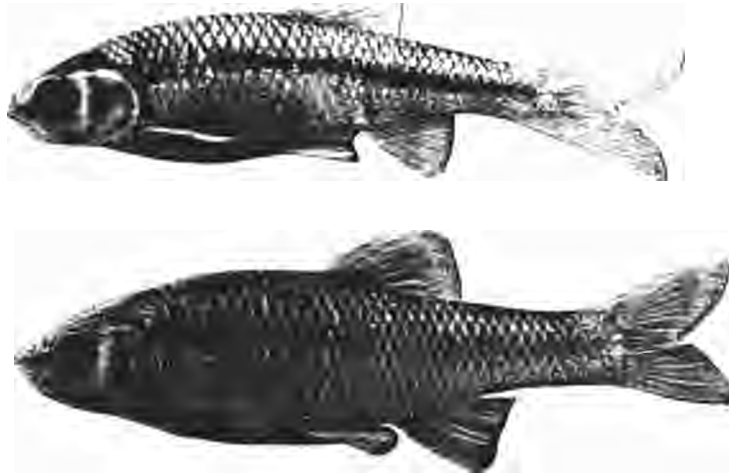


Figure 5. Mature specimens of Notropis lepidus (TU 22263) from headsprings at waterfall, Nueces River, Real County, Texas, 25 July 1954. Upper is a 41 mm SL female, lower is a 55 mm SL, tuberculate male.

Range.—Nueces River system and headwaters of the Guadalupe River system, Texas, U. S. A.; only in streams draining the Edward's Plateau of Texas.

Notropis proserpinus (Girard)

proserpine shiner, Figs. 4, 6.

Moniana proserpina, Girard, 1856: 200 (orig. descr.; co-types in the U. S. National Museum and Museum of Comparative Zoology, Harvard Hubbs and Ortenburger, 1929, Devil's River, Texas), 1859a: 59; Jordan, 1885: 125; Jordan and Evermann, 1896: 272; Fowler, 1910: 280; Hubbs and Ortenberger, 1929: 75; Jordan, et al., 1930: 132.

Moniana aurata, Girard, 1856: 200 (orig. descr.; co-types deposited as for M. proserpina Pubbs and Ortenberger, 1929]. "Piedra-painte, New Mexico"), 1859a: 56; Jordan, 1885: 125; Jordan and Evermann, 1886: 272; Fowler, 1904: 245, 1910: 280.

Cyprinella proseroia, Jordan, 1878b: 421.

Notropis proserpina, Jordan, 1885: 125; Jordan and Evermann, 1886: 272; Fowler, 1904: 245, 1910: 280.

Notropis proserpinus, Hubbs and Ortenberger, 1929: 75; Baughman, 1950: 117-118; Hubbs, 1954: 281, 283, 1956: 463-469, 1957: 93, 1958: 7; Eddy, 1957: 137; Moore, 1957: 64, 1968: 86; Hubbs and Hubbs, 1958: 306; Minckley and Lytle, 1969: 491.

Range.—In, and adjacent to, clear tributaries of the Pecos River, New Mexico (Koster, 1957) and Texas, U. S. A., and of the Rio Grande (Devil's River and San Felipe Springs in Texas, U. S. A., and a stream in northern Coahuila, Mexico) to

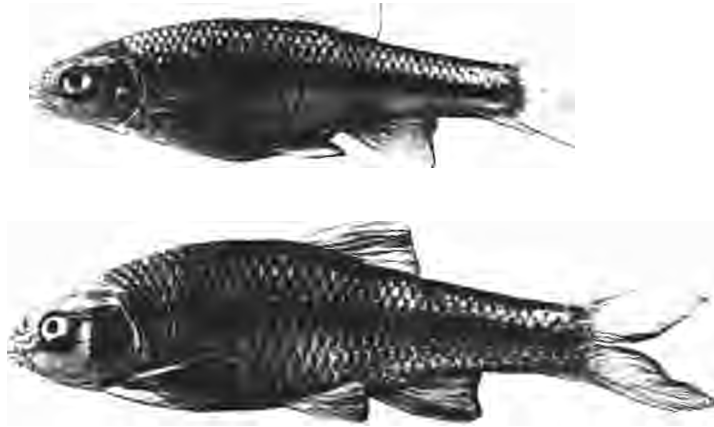


Figure 6. Mature specimens of Notropis proserpinus (ASU 1701) from the Devil's River at Baker's Crossing, Val Verde County, Texas, 11-12 April 1965. Upper is a 44 mm SL female, lower is a 54 mm SL tuberculate male.

approximately half-way between Villa Acuña and Piedras Negras, Coahuila, Mexico (Hubbs, 1954; Robinson, 1957; Minckley, pers. comm.). Much of the habitat formerly occupied by this species now is inundated by the International Amistad Reservoir. The statement by Minckley and Lytle (1969) that no known, valid records of this species supported Koster's (1957) statement of its presence in that state resulted from their missing Moniana aurata Girard as a synonym, from Piedra Pointe, New Mexico. It is interesting that the species seemingly no longer lives in that region of New Mexico, since despite considerable pumping, substantial springs still flow (Minckley, pers. comm.).

Notropis rutilus (Girard)

Salado - San Juan shiner, Figs. 4, 7.

Moniana rutila, Girard, 1856: 201 (orig. descr., co-types at Museum of Comparative Zoology, Harvard [Hubbs and Gordon, ms], Cader-eita, Nuevo Leon, Mexico), 1859a: 57; Jordan, 1885: 125; Hubbs and Ortenberger, 1929: 75; Jordan, et al., 1930: 131.

Moniana gracilis, Girard, 1856: 201 (orig. descr., Monterrey, Nuevo Leon, Mexico), 1859a: 59; Jordan, 1885: 124-125; Hubbs and Ortenberger, 1929: 75; Jordan, et al., 131.

Cyprinella gracilis, Jordan, 1878b: 421.

Cyprinella rutila, Jordan, 1878b: 421.

Cliola montiregis, Cope, 1885: 168 (orig. descr., Monterrey, Nuevo Leon); Jordan, et al., 1930: 131.

Notropis lutrensis, Jordan, 1885: 124-125 (part); Jordan and Evermann,

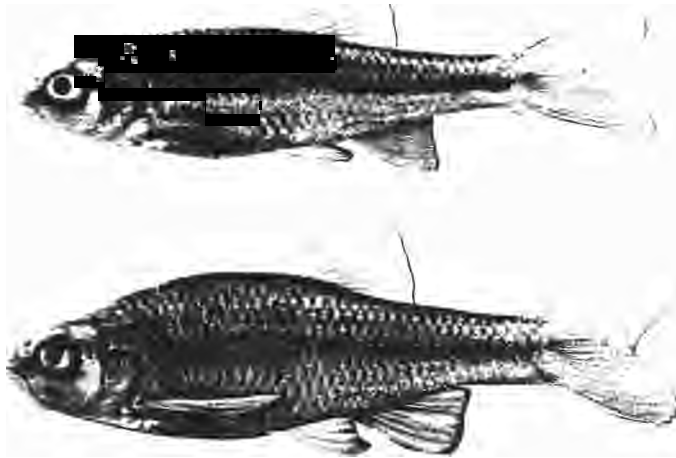


Figure 7. Mature specimens of Notropis rutilus (UNL 616) from unnamed creek 2.5 km southwest El Ranchito, Nuevo Leon Mexico. Upper is a 37 mm SL female, lower is a 39 mm SL, tuberculate male.

1896: 271-272; many others, principally in part.

Moniana lutrensis, Jordan, et al., 1930: 131 (part).

Notropis rutilus, Hubbs and Hubbs, 1958: 306; Contreras B., 1967: 6;

Minckley, 1969: 40; Minckley and Lytle, 1969: 491.

Range.--Rio Salado and Rio San Juan systems, Coahuila, Nuevo Leon,
and possibly Tamaulipas, northeastern Mexico,

Descriptive Comparisons

N. xanthicara and N. rutilus both have shorter heads, on the average, than do the two other species, N. proserpinus and N. lepidus. The snout is much shorter in rutilus, substantiating its snub-nosed aspect, with xanthicara, proserpinus, and lepidus all longer-snouted (Table 3). Interorbital width is least in xanthicara and rutilus, and greatest in the two northern forms, again supporting the visual impression of a narrower xanthicara and rutilus and thicker-bodied proserpinus and lepidus. Length of the orbit is highly variable in xanthicara, but its mean distinguishes the fish as large-eyed when compared to the other species. Both Mexican forms are shallower and narrower in body proportions than are the northern forms, with xanthicara and lepidus occupying their respectively opposing extremes. The caudal peduncle is shallowest in xanthicara and proportionately very short, whereas in rutilus it is deep and long. N. proserpinus is intermediate in these respects, and in lepidus the caudal peduncle is deepest and shortest of the four. Although quite variable, means of pre- and postdorsal and pre- and postpelvic lengths present the

following trends: 1) lepidus has the most posterior dorsal and pelvic fins; 2) rutilus has the most anterior dorsal and pelvic fins; and 3) xanthicara and proserpinus are intermediate, with the former approaching lepidus and the latter approaching rutilus. The oblique measurement of body depth from origin of dorsal fin to origin of anal fin indicates xanthicara as markedly shallower, with the relative depth increasing through rutilus and lepidus to proserpinus (Table 3).

All four species show a proclivity for either 33 or 34 scales in the lateral line (range, 31 - 36; Table 4) 6 scales above the lateral line (5 in xanthicara), and 4 scales below the lateral line (usually 3 in lepidus). They tend to have 8 anal fin-rays, except for 9 in lepidus, and 13 pectoral fin-rays (14 in lepidus).

In all four species, the posterior edge of the maxilla falls below and somewhat short of the anterior margin of the orbit. The mouth in xanthicara is oriented almost vertically, the lower jaw making an abrupt angle with the head (Fig. 3). In proserpinus, the mouth is almost horizontal (Fig. 6). N. rutilus is somewhat intermediate in this feature, with the mouth curved horizontally, having a softly rounded lower jaw (Fig. 7), and lepidus has a semi-horizontal mouth that angles gently upward from the horizontal plane (Fig. 5).

The caudal fin of xanthicara has its upper lobe longer and more expansive than the lower, or the lobes are sub-equal. The other species have the caudal lobes sub-equal in size, or have the lower lobe longer and larger. Pelvic fin lengths are variable. N. xanthicara, the upper Salado form of rutilus, and part of the San Juan form of rutilus have lengths of these fins that range over the distance

Table 3. Means and ranges (in parentheses) for 14 morphometric features of four nominal forms of the *N. proserpinus* group of the genus *Notropis*, subgenus *Cyprinella*. Data are given as thousandths of standard length used as whole numbers

Characters	<i>N. proserpinus</i>	<i>N. rutilus</i>	<i>N. lepidus</i>	<i>N. xanthicara</i>
Length of Head	273 (243-303)	263 (229-302)	279 (250-314)	264 (231-291)
Length of Snout	82 (63-95)	72 (53-90)	81 (65-96)	80 (62-95)
Length of Orbit	85 (64-103)	81 (64-113)	88 (68-103)	90 (64-119)
Interorbital width	92 (77-105)	87 (69-105)	91 (78-103)	86 (69-99)
Predorsal Length	546 (515-589)	533 (500-580)	562 (508-597)	540 (495-595)
Prepelvic Length	52 (475-550)	503 (469-550)	524 (495-568)	519 (486-583)
Depth of Body	243 (98-292)	234 (181-281)	246 (203-278)	209 (178-256)
Width of Body	145 (103-184)	125 (86-174)	144 (104-189)	123 (94-149)
Postdorsal Length	494 (455-546)	502 (461-542)	479 (442-514)	485 (455-552)
Postpelvic Length	514 (468-557)	515 (472-571)	508 (469-541)	499 (466-541)
Length of Caudal Peduncle	238 (202-271)	242 (203-282)	228 (198-267)	230 (188-261)
Depth of Caudal Peduncle	107 (92-135)	113 (90-153)	117 (100-134)	102 (85-132)
Dorsal to Anal Origins	280 (230-334)	271 (232-328)	278 (246-319)	248 (212-287)
Dorsal Origin to Nape	333 (296-364)	331 (290-372)	351 (317-364)	325 (300-370)

Table 4. Percentages of total specimens examined for four nominal forms of the N. proserpinus group of the genus Notropis, subgenus Cyprinella, having numbers of meristic characters listed toward the left.

Character		N. proserpinus	N. rutilus	N. lepidus	N. xanthicara
	32	10	29	20	13
Scales in	33	20	39	40	22
Lateral line	34	49	42	40	65
	35	21	-	----	----
	5				60
Scales Above	6	79	75	87	40
Lateral line	7	21	25	13	---
		25	63	38	43
Scales Below	4	73	33	52	57
	7	10	16		20
Anal	8	90	84		80
fin-rays	9	----	----	90	---
	10		----	10	---
	12		22	18	14
Pectoral	13	49	58	28	51
fin-rays	14	31	20	44	31
	15	20	----	----	

from the vent to the origin of the anal fin. The lower Rio Salado and remaining San Juan forms of rutilus, and lepidus, have pelvic fins that extend almost invariably beyond the origin of the anal fin. N. proserpinus is extremely variable in this feature, with lengths of pelvic fins in various samples reaching to almost any point between the vent to beyond the origin of the anal fin.

Melanophore distribution, albeit variable as discussed before, is quite distinctive for each of the species studied. A blue-black discrete lateral band, passing from the caudal fin to the orbit and onto the snout, is highly diagnostic for N. xanthicara. This band is about two scale rows wide, is interestingly not expressed in the eye, but does extend onto the middle rays of the caudal fin. In the other three species, lateral bands are only variably represented, commencing at either the caudal fin or the hypural crease, passing anteriorly to just below the dorsal fin, or perhaps not that far, where it becomes diffuse. It will sometimes reach the opercle in a broad, diffuse state, sometimes the orbit, but rarely the snout. When in the diffuse state, a thin, 'pencil stripe' is revealed passing approximately along the middle of the lateral band. This stripe has its origin at the hypural crease and typically passes anteriorly over at least two-thirds of the lateral band. In lepidus, it attains its greatest expression in often reaching the opercle.

A dark, basicaudal spot created by a slight widening of the lateral band in N. xanthicara is not separated from the band itself. In rutilus, some proserpinus, and many lepidus, a vertical, thin, unpigmented area separates pigmentation of the caudal fin from the

lateral band itself. In breeding males of all but xanthicara the lateral band may be totally masked by green or aqua-marine pigments. Breeding females, and both sexes in xanthicara, tend to have more intense, well-defined lateral bands when compared to non-reproductive individuals.

There is an ordered representation of a cross-hatched melanophore distribution outlining body scales. In xanthicara, the pattern occurs only above the lateral band. In lepidus, scale markings are above the lateral band but often continue to include scales of the lateral line, but pass no lower on the sides. In rutilus and proserpinus, the patterns extends below the lateral band, to the lateral line, and often below the lateral line to the belly.

The peritoneum in N. xanthicara is black, and may be seen as a diagonal line from the upper edge of the opercle to just behind the pectoral fin, through a thin point in the body wall and also at the midline of the belly. N. xanthicara, otherwise, is immaculate below the lateral band. Peritonea of rutilus and proserpinus are brown and/or silvery with dark mottling and speckling. M. lepidus has a brown peritoneum, with darker mottling and speckling. The peritonea of the last three are not readily discernible through the body walls at any point.

A patch of dark pigment in the gular region, the gular bar, is variably present in xanthicara, ranging from coverage of the anterior third of the gular region to blackening of the total length of the area; muted rays of melanophores connect the bar to the margins of the maxillary corners, in association with a crescent of pigment

that is moderately to heavily present on the upper and lower lips. The gular bar is sometimes present in rutilus and proserpinus, with the lips lightly or not at all dusted with melanophores. In lepidus, the gular bar is absent, and the lips are typically unpigmented.

In xanthicara there is pigmentation over the cranial bones, anterior to the nape, that resembles a heart. Pigment is most dense over the parietal and posterior portion of the frontal bones. This condition also prevails in lepidus. In rutilus, however, the heart-shape is present, but often obscured, and in proserpinus it generally is obscured by other pigmentation or is absent.

The dorsal and caudal fins are the most heavily invested with melanophores in all four species. The dorsal fin in xanthicara and in the upper Rio Salado form of rutilus have only the fin rays delicately outlined. In the lower Rio Salado and San Juan forms of rutilus, and in proserpinus and lepidus, melanophores not only line the rays, but also on the interradial membranes. The last two species have greater numbers of melanophores on their dorsal fins, often causing them to appear sooty in preserved material. The reverse of the above is generally true for melanophore distributions and concentrations on the caudal fin. In all four species at least the leading margins of the caudal fin are outlined by melanophores, and the procurrent rays and middle 4 or 5 rays also are pigmented, particularly so in xanthicara.

The leading ray and interradial membranes of the pectoral fins usually bear a scattering of melanophores in all four species. The anal and pelvic fins lack melanophores in rutilus and lepidus, but bear them along the leading edges in proserpinus and xanthicara. The

base of the anal fin is heavily pigmented in xanthicara, and scarcely pigmented, if at all, in the other forms. All but lepidus have a distinct concentration of melanophores at the base of the dorsal fin.

Tubercle sizes were classed, arbitrarily, as granulate, small, medium, and large. In general, xanthicara had fewer and smaller tubercles than did the other three species. N. proserpinus and lepidus tended to be more tuberculate, both in quantity and size of individual organs. N. rutilus was intermediate.

Concentration of small tubercles over the nape of all four species was highly variable, ranging from complete coverage to absent, and the organs were randomly arranged. The opercles are not tuberculate in xanthicara and the upper Rio Salado rutilus (including Marsh's collections). The remaining lower Salado and Rio San Juan rutilus, and proserpinus and lepidus, have scattered, granulate tubercles on their opercles.

Granulate through large tubercles are present on the snouts of xanthicara, rutilus, and proserpinus. Only small and granulate, rarely medium, tubercles are on the snout of lepidus. A hiatus is present between the snout tubercles and those of the surface of the head in all four species. In xanthicara, it is a strong cleft, but less so than in proserpinus, which has much coarser tuberculation. In rutilus and lepidus, the hiatus is variable, each having samples that display the hiatus as a distinct cleft (Marsh's series, upper Rio Salado rutilus, and Rio Frio lepidus), or as a wide, rippled depression dotted with granulate tubercles (lower Rio Salado and Rio San Juan rutilus and Nueces River lepidus). In proserpinus, tubercle size

decreases progressively over the surface of the head to the nape, and their arrangement is random at final development. Tubercles on the dorsal surface of the head in xanthicara and lepidus are more uniform in size, ranging backward from the snout in two rows and becoming irregularly arranged in the post-ocular region. This condition is also found in the lower Rio Salado and Rio Sabinas de Nuevo Leon forms of rutilus. The upper Rio Salado and distant Rio San Juan stocks of rutilus have the entire dorsal surface of the head covered by irregularly arranged tubercles of medium size.

Granulate tubercles occur on the lips of xanthicara, lower Rio Salado and Rio San Juan rutilus, and also in lepidus and proserpinus. Marsh's collections and the upper Rio Salado rutilus have both small and granulate tubercles on the lips. Granulate tubercles are present on the chin in all four species, but the upper and lower Rio Salado forms of rutilus, and proserpinus, also have small tubercles on the chin. The gular regions of xanthicara and lepidus have only granulate tubercles; rutilus and proserpinus have both granulate and small organs in that region.

N. xanthicara generally lacks tubercles along the anal fin base and on the venter of the caudal peduncle, but when present they most often span the entire region. N. rutilus also is highly variable, with tubercles sometimes occurring only along the anal base, but sometimes extending posteriad to the caudal origin. In proserpinus, tubercles almost invariably are present along the anal fin base and anterior $1/2 - 3/4$ of the caudal peduncle, but never reach the caudal fin. Tuberculation of this region in lepidus almost always includes

at least the anterior half of the caudal peduncle, and usually reaches the caudal fin.

Tuberculation of the dorsal fins of xanthicara and lepidus are expressed as single, small units on all rays; seldom is the dorsal fin devoid of tubercles. The dorsal fins of rutilus and proserpinus either lack tubercles, or have sparsely-scattered, single tubercles on all rays. The caudal and anal fins are never tuberculate in xanthicara, and the same is generally true for lepidus. N. rutilus and proserpinus usually lack tubercles on the caudal fin, have the organs singly disposed on at least the first seven rays of the anal fin. Some fish from samples of the San Juan rutilus have all anal fin-rays tuberculate.

Pectoral fins of xanthicara have tubercles arranged in two rows on the first five rays, at least, and sometimes on the first seven. The lower Rio Salado and Rio San Juan forms of rutilus, and lepidus, have at least the first four rays of the pectoral fins with tubercles in single rows. Marsh's collections, the upper Rio Salado form of rutilus, and proserpinus, have tubercles on rays 1 and 6 in single rows, while the intervening rays, 2 through 5, have tubercles in multiple rows.

ORIGINS AND AFFINITIES

Geologic background

The formation and positions of the larger, present-day structures (e.g., mountain zones, upwarps, etc.) in south Texas, U. S. A., and in northeast Mexico were controlled largely by pre-existing structures, many of which formed as early as the Pre-Cambrian Era (Hurray, 1961).

The region was occupied periodically by the sea during Mesozoic, especially by the relatively-large "Mexican Geosyncline" (Maldonado-Koerdell, 1964), with the last incursion occurring in Oligocene (West, 1964) of the Tertiary Period. Later Cretaceous and early Tertiary sediments reflect a flood of debris from highlands that rose north, west, and south of the ever-declining embayment (Murray, 1961). Sedimentation and subsidence have been relatively continuous in the Gulf Coastal region since early Tertiary (Barnard and LeBlanc, 1965).

Late Mesozoic and early Cenozoic orogenic activities modified the basic simplicity of the seaward-sloping sedimentary mass which flanked the Gulf of Mexico along its northwestern margin. Mountain building compressed segments of the coastal sediments to form, or to resurrect, the northern portion of the Sierra Madre Oriental, and uplift in inland areas re-elevated older elements of the Mesozoic Oachita orogenies; the whole region was generally uplifted. Fracture systems oriented principally northwest - southeast and northeast - southwest, with secondary systems becoming aligned east - west and north - south. Initial movements occurred along the former, older zones of weaknesses, with later, younger fractures relating to the prominent, pre-existing geologic elements, some of which were by now deeply buried by subsequent sedimentation and crustal movements.

The history of integration of the river system now known as the Rio Grande is fragmentary, and must be somewhat conjectural at the present time. However, the lower course of that stream, east of Sierra del Carmen - Chisos Mountains of the Big Bend of Texas, may well have been in existence as far back as the Eocene (King, 1935),

including as its tributaries the many spring-fed streams that rise from the cavernous, water-yielding limestones of southeastern New Mexico and the Edwards Plateau of Texas (including many present tributaries of the Nueces River system, many of which trend suspiciously toward tributaries of the Rio Grande, only to divert eastwardly). Rio Salado and Rio San Juan of Mexico also arise from **springs**, in the main, and in more well-watered times would have combined with the others to form a substantial river system, with at least seasonally clear waters despite the large amount of debris that it apparently carried to coastal deposition (King, 1935).

Late Tertiary deposits of river gravels near Albuquerque, New **Mexico**, indicate, on the other hand, that a major, south-flowing river existed there, at least as far back as Miocene (King, 1935). The evidences for this stream(s) south of Albuquerque are obscured by sedimentation in basins, and by erosion of mountain masses, which were formed during a period of relatively-intense faulting during Mio-Pliocene times in the area now known as Trans-Pecos Texas (an area bounded by mountains west of the Pecos River, mountains along **the southern** edge of the Basin and Range Province of the U. S., and by the eastern edge of the Sierra Madre Oriental of Mexico). During and after this period of tectonic activity, sediments were laid down in the basins to great thickness, and there is no evidence that the basins were connected by any large **streams**. It is hypothesized (King, 1935) that the stream originating in the **southern** Rocky Mountains flowed south through unknown channels to empty into the basin of Lago de Guzman, northern Chihuahua, Mexico, and that filling of

large depression, and associated basins, allowed integration of the upper, ancestral Rio Grande with the lower portion, through a process of basin filling, cutting of pediments, basin filling, more cutting, and so on.

An alternative view, supported in part by some of King's (1935) data itself, is that pediment cutting was unidirectional, since antecedent channels of an ancient Rio Grande system were already available through which waters might pass. Basins whose waters rise high above their floors generally cut recognizable shoreline features because of a time of stabilization at outlet level, and none of the basins of Trans-Pecos Texas, or southern New Mexico, known to me, bear such evidences (Hubbs and Miller, 1948; Kottlowski, 1958; Minckley, 1969, and references cited). King (1935) notes that tectonic movements apparently took place along the faults of northern Trans-Pecos Texas, whereas few or none of these structures in southern Trans-Pecos Texas were affected. The last also seems the case in northern Mexico, at least in the northern part of the Sierra Madre Occidental, and in the great Bolson de Mapimi, as far south as Parras, Coahuila (Imlay, 1936; Kellum, 1936, Kelly, 1936, and references cited). Notwithstanding the manner of integration, or re-integration of the system, final connection between the upper and lower segments of the Rio Grande was not realized prior to mid-Pleistocene times, on the basis of present information, and its subsequent history has been one of downcutting (King, 1935; Kottlowski, et al., 1965).

The Pecos River, after (or during) deposition of the Pliocene Plains radiating out from the Rocky Mountain uplift, eroded northward

to behead upper tributaries of the Colorado, Brazos, and Canadian rivers, and probably some of the tributaries of the ancient upper Rio Grande. The reasons for its north - south orientation over such unconsolidated sediments are obscure, and it crosses no mountain barriers as does the Rio Grande (King, 1935). In Texas, the Pecos flows generally parallel to the Rio Grande, probably following structural features of the underlying strata. Most tributaries to the Pecos River flow into it from the west, in its upper half in New Mexico. Springs, and the sediments through which it flows in its lower part impart considerable salinity to its waters, a factor which at present at least, forms somewhat of a barrier to certain aquatic animals, but appears to enhance the occurrence of others of estuarine affinities.

The lower course of the Pecos may flow in an ancient, antecedent channel, as is suggested for the Rio Grande above and through the Big Bend, and for some distance below.

Faunal Evidence for an Integrated, Disrupted, and Re-connected Rio Grande system

Literature on systematic ichthyology is permeated with the concept that the fish species and genera that we see today evolved in the Pleistocene Epoch, a relatively short period of geologic time, and that geographic isolation in arid and semi-arid zones has allowed rapid, and somewhat chaotic, evolution. However, a number of recent papers, Mille (1965, 1968); Uyeno and Miller (1963, 1965), to name a few on western North American fishes, tend to place such origins back in time, to Pliocene or even perhaps into Miocene. This allows

considerably more flexibility in interpretation of relationships, not only of fishes (some of which have seemingly remained remarkably unchanged, as based on comparisons of fossil with Recent materials), but also of the drainage relations of regions, as indicated by the fishes, and other aquatic organisms. This expanded outlook is used here, in part at least, in discussing the origins and relations of the complex of Notropis studied, a discussion (tentative at best) of the N. lutrensis complex on the Mexican Plateau and less confidently elsewhere, and of other animals that seem to indicate the sequence of development of the present-day Rio Grande system.

The relationships of the complex studied by me, N. lepidus, rutilus, xanthicara, and proserpinus, to the "lutrensis-group" of Gibbs (1957a) must first be examined. There can be little doubt as to their correct placement in the subgenus Cyprinella, since the following features of all four species are shared with other, more eastern forms: 1) the exposed margins of the lateral scales are higher than wide and are (variably) lined with melanophores, appearing diamond-shaped; 2) the fins of nuptial males contain a milky deposition, the only feature determined by Gibbs to be invariable in the subgenus; 3) the origin of the dorsal fin is just behind the insertion of the pelvic fins; 4) dorsal and pelvic fin-rays number eight in all four species (not treated further here); and 5) a hiatus is present between snout and head tubercles in nuptial males of all four species. The species studied by me also had a number of exceptions to the general diagnosis of Cyprinella; Gibbs also found these exceptions in widely-scattered species treated by him, and considered them secondarily derived or

or deleted, or primitive. The major exceptions in the four lower Rio Grande species were loss of a tendency for concentration of melano-phores in the posterior part of the dorsal fin (all four), a strong tendency toward 4 - 4 pharyngeal teeth (complete in proserpinus, lepidus, and xanthicara; 3 of 74 rutilus had a single, weak tooth in one or the other outer row), rather than 1-4 - 4-1, some variation from the "norm" in predorsal circumferential scales and caudal peduncle scales (not treated further here), and either a linear (primitive; lepidus and xanthicara) or scattered (advanced; proserpinus and rutilus) distribution of nuptial tubercles.

Gibbs (1957a) deemed N. spilopterus (Cope) as the most likely ancestor of the "lutrensis group," through isolation in "Texas or elsewhere in the southwestern United States and consequent dispersal of the newly-evolved form into Mexico, where further differentiation took place." The two subspecies of spilopterus, N. s. spilopterus generally east of the Mississippi River and N. s. hypsomatus Gibbs in the Ozarks and upper Mississippi River tributaries, have yellow (if not blackened) fins in breeding males, and a number of other features (Gibbs, 1957b), that make them likely candidates (especially the western form) as basilar stock from which proserpinus, rutilus, xanthicara, and lepidus evolved. N. spilopterus, or its progenitor is thought to have given rise to another yellow-finned Cyprinella, N. venustus in coastal drainages east of the present Mississippi River, which then dispersed along the coast to become broadly sympatric with all but xanthicara of the four species studied by me, plus a number of other Cyprinella (Gibbs, 1957a, c). N. v. venustus hybridizes

with lepidus in the Guadalupe River system, Texas (Hubbs, 1954), as mentioned before, and with the coastal form (N. 1. suavis; Hubbs, et al., 1953; Hubbs, 1954) and Plains form (N. 1. lutrensis; Minckley, pers comm., Las Moras Creek, near Bracketville, Texas) of the red shiner. The intense, black, basicaudal spot of N. v. venustus makes it easily distinguished from other Cyprineila in zones of sympatry.

The differentiation of the four species treated here from other kinds of Cyprinella comprises a mosaic of characteristics that almost totally spans the spectrum of characters used by Gibbs (1957a-c, 1961, 1963) in his treatment of the 15 or so eastern species. He considered the Mississippi River and its tributaries as a 'hub' for the dispersal of the group, about which variously-differentiated forms were arranged. The features in common between the four Rio Grande species indicate them to be closely-knit among themselves, but the diversity of divergent features makes interpretation of their relations to other species of the subgenus quite difficult. Quantification of features of the four species as done by Gibbs (1957a: Table 1), insofar as was possible, produced an "index of similarity" of approximately 4 between xanthicara and spilopterus, 7 between lepidus and spilopterus, 8 between rutilus and the last species, and 5 between proserpinus and spilopterus. Attempts to construct "indices of similarity" between forms of N. lutrensis and the four Rio Grande forms were equally unproductive; however, similarity values were generally lower between the pairs that were contrasted. I can only conclude that selection pressures on the Rio Grande forms caused them to differentiate locally and rapidly, or that they penetrated to the region of

the Rio Grande system quite early in the dispersal of the group, and represent one of the older, relict species groups of the subgenus. There seems adequate data, on fishes and other kinds of aquatic animals in northern Mexico, to support the latter conclusion, and it is pursued further below. I tend toward a somewhat different interpretation of the "lutrensis group" of Cyprinella than that given by Gibbs, and exclude the yellow-finned, lower Rio Grande forms from it. It seems most likely that they are an independent derivative from the N. spilopterus type of Cyprinella.

The "lutrensis group" is therefore re-defined as including N. lutrensis and its derivatives in Mexico, exclusively, most of which are to be discussed later. Similarities between lutrensis and the more-western populations of N. spilopterus, although possibly in part a result of hybridization (Gibbs, 1957a-b), strongly indicate derivation of the former from the latter, most likely in the Plains Region. The erosive, fluctuant Plains streams should have given rise to an aggressive, successful, and variable Cyprinella, which N. lutrensis certainly appears to be, and its entry into Coastal streams of Texas, and invasion of the Mexican Plateau, appear reasonably explicable on the basis of data now at hand.

At an early stage, I suggest that the Rio Grande may have been a highly integrated drainage system, including not only its present drainage in the United States, but a vast area of north-central Mexico. This may serve to explain, in part, the large amount of debris that has been deposited by the stream in the western Gulf of Mexico (Murray, 1961). It also may have had strong western affinities in its

fauna, with little influence from the presumably-complex ichthyofauna of what now is the Mississippi River basin, a fauna that now dominates the mainstream Rio Grande. The presence of Rhinichthys cataractae (Valenciennes), Gila modesta (Garman), and perhaps Dionda episcopa Girard, in the Rio San Juan system (Meek, 1904; Contreras B., 1967), the first two of which are related north and west, respectively, may document this phase, as may the presence of a western hydrobiid snail genus, Fontilicella, in springs of a tributary of the San Juan near Saltillo, Coahuila (J. J. Landye, pers. comm.). R. cataractae, however, persisted in the mainstream Rio Grande as far downstream as Laredo, Texas, in the 1950s (Robinson, 1959). Gila pandora (Cope), generally distributed in the upper Rio Grande and Pecos River, now is known from a relict population in the Davis Mountains, Texas (Miller and Hubbs, 1962), and may also be included as an indicator of an ancient, through-flowing stream. At this time, it is assumed that Cyprinella had not entered the upper Rio Grande, and that the Pecos had not yet succeeded in its northward cutting to behead Gulf Coastal streams or those tributary to the zone now drained by the Mississippi.

Uplift in the southeast - northwest trending mountains of Texas could then have diverted the Rio Grande headwaters to the south (King, 1935), into the Guzman depression, or perhaps farther along what now is the Coahuila - Chihuahua border (Meek, 1904). This would have allowed other fishes of western affinity, Pantosteus plebeius (Baird and Girard), and progenitors of other coarse-scaled Gila (now perhaps represented by G. nigrescens [Girard], G. pulchra [Girard], G. conspersa Garman, and others), plus a number of western genera

of hydrobiid molluscs, and even sphaeromatid isopods (Landye and Minckley, pers. comm.), access to the Mexican Plateau (or movement in the reverse direction). Uplift in the Rocky Mountain area of origin of this ancestral stream also may have stimulated headward erosion, and capture of Plains streams such as the Arkansas River, through which a lutrensis-like fish could have moved downward to the Guzman basin, there to evolve the plethora of nominal forms presently referred to N. formosus (Girard), which ultimately gained access to the Rio Yaqui system of the Pacific drainage of Mexico (N. f. mearnsi Snyder).

During this interval of disruption of the Rio Grande mainstream, a spilopterus-like fish must have moved coast-wise to inhabit independent drainages from west of the Mississippi southward to the Rio Grande, or, more likely perhaps, it moved by lateral stream captures between relatively-clear, spring-fed watercourses. With it may well have moved a lutrensis-like form, to develop in the coastal drainages the shallow-bodied N. 1. suavis north of the Rio Grande, a similarly-shaped kind south of the Rio Grande, N. 1. forlonensis (Meek) (Rivera T., 1971), and perhaps some similar kind in the Rio Grande itself, now extinct.

Re-integration of the Rio Grande system in mid-Pleistocene (Kottowski, et al., 1965), accompanied by rapid northward cutting by the Pecos, isolation of the Guzman basin, and development of the large Rio Conchos system of Chihuahua, Mexico (which may have been part of a south-flowing system in the preceeding stage, diverted north and greatly increased in size by uplift in the Sierra Madre Occidental), provided access to the lower Rio Grande system, the Pecos, and by

upstream invasion the upper Rio Grande and Rio Conchos, for Plains and some "big-river" components of the vast Mississippi River fauna. Included was the deep-bodied, aggressive, red shiner of the Plains, N. 1. lutrensis. It almost penetrated into the Guzman system, via tributaries of the Rio Conchos, since material from the Sauz Basin, Chihuahua (Minckley and Koehn, 1965), almost certainly represents a stabilized hybrid swarm, or intergrades, between the Conchos form of lutrensis and N. formosus (Contreras B., pers. comm.). A deep-bodied lutrensis, N. 1. garmani (Jordan), occurs in the now-isolated rios Nazas and Aguanaval, Mexico. N. 1. lutrensis now abounds through the Rio Grande system, from its upper parts to Brownsville, Texas (Koster, 1957; Robinson, 1959; Moore, 1968). It intergrades with N. 1. forlonensis in the Rio San Fernando, eastern Mexico (Rivera T., 1971), but apparently has not moved northeast along the Texas Coast (Hubbs, 1954).

Relicts of the upper Rio Grande system (or of the ancient river) now occur generally in its headwaters (G. pandora, P. lebeius, and R. cataractae) and have spread, in part, to the headwaters of the Pecos River. Those of the lower portion, such as the minnows I studied, Dionda episcopa, and a number of other forms, have generally been pushed upstream into springs or spring-fed refugia inhospitable to the more generalized Mississippi River fishes, or they persist in the isolated springs in which they presumably evolved (i.e., in the Cuatro Ciénegas area, Coahuila). If any western American fishes, such as mainstream forms of Gila, Pantosteus, etc., were present at the time of arrival of the Mississippi River fishes, they would have

rapidly disappeared if the pattern now occurring in the Colorado River basin of western North America is any indication (Miller, 1961; Minckley and Deacon, 1968; Deacon and Minckley, 1972). The general absence of "big-river" endemic fishes in the Rio Grande system, numbering no more than 6 or 7 (described and undescribed), would also seem to substantiate relatively recent invasion by Mississippi River fishes, as does, in a reciprocating manner, the substantial endemism in tributaries and evident "ecological allopatry," often seemingly self-imposed between the presumed ancestral faunal elements and the more recent invaders.

LITERATURE CITED

- Baughman, J. L. 1950. Random notes on Texas fishes, Part 1. Texas J. Sci. 2: 117-138.
- 1965.
- Bernard, H. A., and R. J. LeBlanc. Resume of the Quaternary geology of the northwestern Gulf of Mexico Province. In: The Quaternary of the United States, H. E. Wright and D. G. Frey, eds., pp. 137-18, Princeton Univ. Press, Princeton, New Jersey.
- Contreras Balderas, Salvador. 1967. Lista de peces del Estado de Nuevo Leon. Cuadernos del Instituto de Investigaciones Cientificas, Universidad Autonoma de Nuevo Leon 11: 1-12.
- Deacon, J. E., and W. L. Minckley. 1972. Desert Fishes. In Desert Biology, Volume II, G. W. Brown, ed., Academic Press, New York and London, in press.
- Eddy, S. 1957. How to know the Freshwater Fishes. Wm. L. Brown Co., Dubuque, Iowa.

- Estabrook, G. F. 1966. A mathematical model in graph theory for biological classification. *J. Theoret. Biol.* 12: 297-310.
- _____, and D. J. Rogers. 1966. A general method of taxonomic description for a computed similarity measure. *Bioscience* 16: 789-793.
- Fowler, H. W. 1904. Notes on fishes from Arkansas, Indian Territory, and Texas. *Proc. Acad. Nat. Sci. Philadelphia* 242: 249
- _____. 1910. Notes on the variations of some species of the genus Notropis. *Ibid.* 248: 273-293.
- Gibbs, R. H., Jr. 1957a. Cyprinid fishes of the subgenus Cyprinella of Notropis. I. Systematic status of the subgenus Cyprinella, with a key to the species exclusive of the lutrensis - ornatus complex. *Copeia* 1957: 185-195.
- _____. 1957b. *Ibid.* II. Distribution and variation of Notropis spilopterus, with the description of a new subspecies. *Lloydia* 20: 186-211.
- _____. 1957c. *Ibid.* III. Variation and subspecies of Notropis venustus. *Tulane Stud. Zool.* 5: 175-203.
- _____. 1961. *Ibid.* IV. The Notropis galacturus - camurus complex. *Am. Midl. Nat.* 66: 337-354.
- _____. 1963. *Ibid.* V. The Notropis whipplei - analostanus - chloristius complex. *Copeia* 1963: 511-513.
- Girard, C. F. 1856. Researches upon the cyprinoid fishes inhabiting the fresh-waters of the United States of America west of the Mississippi valley. from specimens in the Museum of the Smithsonian Institution. *Proc. Acad. Nat. Sci. Philadelphia* 8: 165-213,

- _____. 1859a. Fishes. In: Report on the United States and Mexican Boundary Survey, made under the direction of the Secretary of the Interior, by Wm. H. Emory, Major, 1st Cavalry, and the U. S. Commissioner. U. S. Dept. Interior 2: 1-85.
- _____. 1859b. Reports of explorations and surveys to ascertain the most practicable and economic route for a railroad from the Mississippi River to the Pacific Ocean. U. S. House of Representatives, Executive Document 91, Volume 10 (in part by Girard, general résumé of Girard, 1859a).
- Holden, P. B., and C. B. Stalnaker. 1970. Systematic studies of the cyprinid genus *Gila*, in the upper Colorado River basin. *Copeia* 1970: 409-420.
- Hubbs, C. L., and C. Hubbs. 1958. *Notropis saladonis*, a new cyprinid fish endemic in the Rio Salado of northeastern Mexico. *Ibid.* 1958: 297-307.
- _____, and K. F. Lagler. 1964. Fishes of the Great Lakes Region. Cranbrook Inst. Sci. Publ. 26: 1-224 (revised).
- _____, and R. R. Mearns. 1948. The zoological evidence. Correlation between fish distribution and hydrographic history in the desert basins of western United States. *Bull. Univ. Utah*, 38, Biol. Ser. 10: 17-166.
- _____, and _____ 1965. Studies of cyprinodont fishes. XXII. Variation in *Lucania parva*, its establishment in western United States, and description of a new species from an interior basin in Coahuila, Mexico. *Misc. Publ. Univ. Mich. Mus. Zool.* 127: 1-111.

- _____, and A. I. Ortenberger. 1929. Fishes collected in Oklahoma and Arkansas in 1927. *Publ. Univ. Okla. Biol. Surv.* 1: 45-112.
- Hubbs, C. 1951. Observations on the breeding of *Dionda episcopa serena* in the Nueces River, Texas. *Texas J. Sci.* 3: 490-492.
- _____. 1954. Corrected distributional records for Texas freshwater fishes. *Ibid.* 6: 277-291.
- _____. 1956. Relative variability of hybrids between the minnows, *Notropis lepidus* and *N. proserpinus*. *Ibid.* 8: 463-469.
- _____. 1957. Distributional patterns of Texas freshwater fishes. *SW Nat.* 2: 89-104.
- _____. 1958. A checklist of Texas freshwater fishes. Texas Game and Fish Comm., IF Ser. (*Div. Inland Fisheries*) 3: 1-14.
- _____, and K. Strawn. 1956. Interfertility between two sympatric fishes, *Notropis lutrensis* and *Notropis venustus* (*Cyprinidae*). *Evolution* 10: 341-344.
- _____, R. A. Kuehne, and J. C. Ball. 1953. The fishes of the upper *Guadalupe River*, Texas. *Texas J. Sci.* 5: 216-244.
- Imley, R. W. 1936. Evolution of the Coahuila Peninsula, Mexico. IV. Geology of the western part of the Sierra de Páscar. *Bull. Geol. Soc. Am.* 47: 1091-1152.
- Jordan, D. S. 1878a. A catalog of the fishes of the freshwaters of North America. *Bull. U. S. Geol. and Geogr. Surv. Terr.* 4: 407-414.
- _____. 1878b. Distribution of freshwater fishes of the United States'. *Ann. N. Y. Acad. Sci.* 1: 92-120.

1885. Identification of the species of Cyprinidae and Catostomidae described by Dr. Charles Girard, in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1856. Proc. U. S. Nat. Mus. 1885: 118-127.
- _____, and B. W. Evermann. 1896. The fishes of North and Middle America. U. S. Nat. Mus. Bull. 47: 1-1240.
- _____, and H. W. Clark. 1930. A Checklist of the fishes and fish-like vertebrates of North and Middle America, north of the northern boundary of [Venezuela](#) and Colombia. Rept. U. S. Fish Comm. 1928: 1-670.
- King, P. B. 1935. Outline of structural development of trans-Pecos Texas. Bull. Am. Assn. Petrol. Geol. 19: 221-261.
- Kellum, L. B. 1936. Evolution of the Coahuila Peninsula, Mexico. III. Geology of the mountains west of the Laguna District. Bull. Geol. Soc. Am. 47: 1029-1090.
- Kelly, W. A. 1936. Ibid. II. Geology of the mountains bordering the valleys of Acatita and las Delicias. Ibid.: 1009-1038.
- Koehn, R. K. 1965. Development and ecological significance of nuptial tubercles of the red shiner, Notropis lutrensis. Copeia 1965: 462-467.
- _____, and W. L. Minckley. 1965. Changes with growth in selected body proportions of the cyprinid fish Notropis lutrensis. SW Nat. 10: 151-155.
- Koster, W. J. 1957. Fishes of New Mexico. Univ. New Mexico Press, ~~Albuquerque~~, New Mexico.
- Kottlowski, F. E. 1958. Lake Otero--second phase in formation of New Mexico's gypsum dunes. Bull. Geol. Soc. Am. 69: 1733-1734.

- _____, M. E. Cooley, and R. V. Ruhe. 1965. Quaternary geology of the Southwest. In The Quaternary of the United States, H. E. Wright and D. G. Frey, eds., Princeton Univ. Press, Princeton, New Jersey. Pp. 287-298.
- Maldonado-Koerdell, M. 1964. Geohistory and paleogeography of Middle America. In: Handbook of Middle American Indians, Volume I. Natural Environments and Early Cultures, R. G. West, ed., pp. 3-32. Univ. Texas Press, Austin, Texas.
- Mayr, E. 1970. Populations, Species, and Evolution. Harvard Univ. Press, Cambridge, Massachusetts.
- Meek, S. E. 1903. Distribution of the freshwater fishes of Mexico. Am. Nat. 37: 771-784.
- _____. 1904. The freshwater fishes of Mexico north of the Isthmus of Tehuantepec. Publ. Field. Columbian Mus., Zool. Ser. 5: i-lxlv, 1-252.
- Miller, R. R. 1968. Two new fishes of the genus Cyprinodon from the Cuatro Ciénegas basin, Coahuila, Mexico. Occ. Pap. Mus. Zool. Univ. Mich. 659: 1-15.
- _____. 1965. Quaternary fresh-water fishes of North America. In, The Quaternary of the United States, H. E. Wright and D. G. Frey, eds., pp. 569-581. Princeton Univ. Press, Princeton, New Jersey.
- _____, and C. Hubbs. 1962. Gila pandora, a cyprinid fish new to the Texas fish fauna. Texas J. Sci. 14: 111-113.
- _____. 1963. Gila pandora, a new cyprinid fish from Coahuila, Mexico, with special reference to the aquatic biota. Texas Western Press, Univ. Texas, El Paso, Sci. Ser. 2: 1-65.

- _____, and J. E. Deacon. 1968. Southwestern fishes and the enigma of "endangered species." *Science* 159: 1424-1432.
- _____, and R. K. Koehn. 1965. Re-discovery of the fish fauna of the Sauz Basin, northern Chihuahua, Mexico. *SW Nat.* 10: 313-315.
- _____, and G. L. Lytle. 1969. Notropis xanthicara, a new cyprinid fish from the Cuatro Ciénegas basin, north-central Mexico. *Proc. Biol. Soc. Wash.* 82: 491-501.
- Moore, G. A. 1957. Fishes. In: *Vertebrates of the United States*, W. F. Blair, ed., pp. 31-210. McGraw-Hill Publishing Co., New York.
- _____. 1968. Fishes. In: *ibid.* (2nd edition). Pp. 21-165.
- Murray, G. E. 1961. *Geology of the Atlantic and Gulf Coastal Province of North America*. Harper and Brothers Publishing Co., New York.
- Rivera Teillery, R. 1971. *Ichthyofauna de los rios San Fernando y Soto la Marina, Estados de Nuevo Leon y Tamaulipas, Mexico*. Unpubl. Biologo Tesis, Universidad Autonoma de Nuevo Leon.
- Robinson, D. T. 1959. The ichthyofauna of the lower Rio Grande, ~~Texas~~ and Mexico. *Copeia* 1959: 253-256.
- Uyeno, T., and R. R. Miller. 1963. Summary of late Cenozoic freshwater fish records for North America. *Occ. Pap. Mus. Zool. Univ. Mich.* 631: 1-34.
- _____, and _____. 1965. Middle Pliocene cyprinid fishes from the Bidahochi formation, Arizona. *Copeia* 1965: 28-41.
- Val Guerra, L. 1952. *Ichthyological survey of the Rio Salado, Mexico*. Unpubl. M.S. Thesis, University of Texas, Austin, Texas.

West, R. G. 1964. Surface configuration and associated geology of Middle America. In: Handbook of Middle American Indians, Volume I, Natural Environments and Early Cultures, R. G. West, ed., pp. 33-83. Univ. Texas Press, Austin, Texas.

Wirth, M., G. F. Estabrook, and D. J. Rogers. 1966. A graph theory model for systematic biology, with an example for the Oncidiinae (Orchidaceae). *Systemat. Zool.* 15: 59-69.

APPENDIX A. Characters and designated character states

Morphometric features as thousandths
of SL, expressed as whole numbers

1. HEAD LENGTH

1 246 - 253
2 254 - 260
~~3~~ 261 - 275
4 276 - 284
5 285 - 292

7. BODY DEPTH

1 190 - 205
2 206 - 219
~~3~~ 220 - 246
~~4~~ 247 - 256
~~5~~ 257 - 271

2. SNOUT LENGTH

1 65 - 68
2 69 - 72
~~1~~ 73 - 81
~~4~~ 82 - 86
~~5~~ 87 - 92

8. BODY WIDTH

~~1~~ 104 - 113
~~2~~ 114 - 120
~~3~~ 121 - 141
4 142 - 152
153 - 176

3. ORBITAL LENGTH

~~1~~ 71 - 78
~~2~~ 79 - 82
~~3~~ 83 - 89
~~4~~ 90 - 96
97 - 107

9. POSTDORSAL LENGTH

~~1~~ 465 - 471
~~2~~ 472 - 481
~~3~~ 482 - 500
~~4~~ 501 - 507
5 508 - 521

4. INTERORBITAL WIDTH

~~1~~ 78 - 82
~~2~~ 83 - 85
~~3~~ 86 - 90
~~4~~ 91 - 93
5 94 - 96

10. POSTPELVIC LENGTH

~~1~~ 476 - 487
~~2~~ 488 - 501
~~3~~ 502 - 517
4 518 - 523
5 524 - 539

5. PREDORSAL LENGTH

1 511 - 527
2 528 - 534
~~3~~ 535 - 551
4 552 - 565
566 - 576

11. CAUDAL PEDUNCLE DEPTH

1 95 - 101
2 102 - 106
107 - 115
7 116 - 121
- 170

6. PREPELVIC LENGTH

~~1~~ 487 - 495
~~2~~ 496 - 504
505 - 521
4 522 - 529
5 530 - 538

12. CAUDAL PEDUNCLE LENGTH

~~1~~ 214 - 220
~~2~~ 221 - 229
~~3~~ 230 - 243
4 ~~244~~ - 249
5 250 - 271

Morphometric features, continued

13. DORSAL- TO ANAL-FIN ORIGIN

- 1 234 - 245
- 2 246 - 258
- 3 259 - 282
- 4 283 - 290
- 5 291 - 299

14. DORSAL-FIN ORIGIN TO NAPE

- 1 317 - 321
- 2 322 - 326
- 3 327 - 339
- 4 340 - 352
- 5 353 - 364

Meristic features

15. SCALES IN THE LATERAL LINE

- 1 32.9 - 33.4
- 2 33.5 - 34.4
- 3 34.5 - 36.3

16. SCALES ABOVE THE LATERAL LINE

- 1 5.0 - 5.4
- 2 5.5 - 6.4

17. SCALES BELOW THE LATERAL LINE

- 1 2.6 - 3.4
- 2 3.5 - 4.0

18. ANAL FIN-RAYS

- 1 7.4 - 8.4
- 2 8.5 - 9.0

19. PECTORAL FIN-RAYS

- 1 11.0 - 12.4
- 2 12.5 - 13.4
- 3 13.5 - 14.4
- 4 14.5 - 15.0

Qualitative Features

20. SHAPE OF CAUDAL FIN

- 1 lobes equally developed
- 2 upper lobe larger
- 3 lower lobe larger

21. LENGTH OF PELVIC FIN

- 1 from vent to origin of anal fin
- 2 from origin of anal fin to beyond its origin
- 3 as in #1 to beyond origin of anal fin

22. LENGTH OF PECTORAL FIN

- 1 not reaching pelvic-fin insertion
- 2 as above to reaching pelvic-fin insertion
- 3 as in #1 to reaching beyond pelvic-fin insertion

23. LATERAL BAND

- 1 absent
- 2 from caudal fin anterior to orbit or snout
- 3 from caudal base to opercle or orbit

24. LATERAL "PENCIL STRIPE"

- 1 absent
- 2 from caudal base anterior to short of opercle
- 3 from caudal base to opercle

25. SPOT ON CAUDAL PEDUNCLE

- 1 absent
- 2 present

26. CROSS-HATCHING ON SCALES

- 1 only above lateral band
- 2 above lateral band and on pored lateral-line scales
- 3 above and below lateral band and pored lateral-line

Qualitative features, continued

27. PIGMENTATION OF DORSAL FIN 35. PREDORSAL BAND
- 1 rays outlined only
2 as in #1, plus interradial membranes pigmented
- 1 well developed
2 poorly developed
28. PIGMENTATION OF CAUDAL FIN 36. POSTDORSAL BAND
- 1 on procurrent rays and leading margins, heavy on middle 4-5 rays, other rays and inter-radials moderate to light
2 on leading margins only, middle 4-5 rays, other rays, and interradials as in #1
3 none
- 1 well developed
2 poorly developed
29. PIGMENTATION OF ANAL FIN 37. PERITONEUM
- 1 absent
2 rays lightly outlined
- 1 black
2 silvery, with mottling or speckling
3 brownish, with mottling or speckling
30. PIGMENTATION OF PELVIC FINS 38. GULAR BAR
- 1 absent
2 rays outlined and/or inter-radials speckled
3 leading margin only
- 1 total, continuous or discontinuous
2 broken, discontinuous or essentially absent
3 absent
4 #1-3 all present
31. PIGMENTATION OF PECTORAL FINS 39. PIGMENTATION OF DORSUM OF HEAD
- 1 absent
2 leading edge or ray
leadina edgd or ray, plus interradials speckled
- 1 distinct "heart" present
· obscured "heart"
3 none
4 #1 or 2 present
32. PIGMENTATION OF ANAL FIN-BASE 40. PIGMENTATION OF UPPER LIP
- 1 present
2 absent
- 1 none or lightly dusted
2 moderately dusted
3 darkened
33. PIGMENTATION OF DORSAL FIN-BASE 41. PIGMENTATION OF LOWER LIP
- 1 present
2 absent
- 1 none or lightly dusted
moderately dusted
3 darkened
34. HUMERAL BAR 42. TUBERCULATION
- 1 present
2 absent
- 1 anteriorly An 2 rows, irregular posteriorly

Qualitative features, continued

42. TUBERCULATION OF HEAD,
continued

- 2 ~~irregular~~ over-all
small at nape, increasing to
large at snout

43. TUBERCULATION OF NAPE

- 1 extensive to origin of
dorsal fin
- 2 1/3-3/4 of nape tuberculate
- 3 none

44. TUBERCULATION OF OPERCLES

- 1 none
- 2 scattered granulate

45. TUBERCULATION OF CHIN

- 1 granulate only
- granulate and small

46. TUBERCULATION OF LIPS

- 1 granulate
- 2 granulate and small

TUBERCULATION OF SNOUT

- 1 granulate
- 2 granulate, small and medium
- 3 granulate, medium, and large

48. TUBERCULATION OF GULAR AREA

- 1. granulate
- 2 granulate and small

49. TUBERCULATION OF ANAL FIN-BASE

- 1 fin-base only
 - 1/2-3/4 of caudal peduncle
- 3 to caudal origin
- 4 none

50. TUBERCULATION OF DORSAL FIN

- 1 lightly or singly on all rays
- 2 none

51. TUBERCULATION OF CAUDAL FIN

- 1 scattered singly
- 2 none

52. TUBERCULATION OF ANAL FIN

- 1 none
- 2 all rays
- 3 1-7 fin-rays
- 4 1-4 or 5 fin-rays

53. TUBERCULATION OF PELVIC FINS

- 1 none
- 2 1-3 fin-rays
- 3 5 or more fin-rays

54. TUBERCULATION OF PECTORAL FINS

- 1 1-5 or more fin-rays in 2
rows
- 2 1, 6 or more singly; 2-5 or
more multiply
- 3 none
- 4 1-4 or more in single rows

APPENDIX B. Provenance of materials utilized

Notropis xanthi caraCUATRO CIENEGAS BASIN

Laguna de los Fresnos--KU 7421

Canal de La Angostura--ASU 945; KU 7404, 7429, 7374

Rio Mesquites--ASU 969, 2268; KU 7394, 7363; UNL 703, 709, 714

Laguna de Churince--ASU 2316, 2332

Notropis rutilusCUATRO CIENEGAS BASIN

Marsh's Collections--UMMZ 130377, 130378

RIO SALADO SYSTEM

Rio Salado de los Nadadores--ASU 913, 1732; TNHC 5986; UMMZ 179820;
UNL 688, 697

Mainstream, Monclova - Hermanas area--ASU 264; KU 7347; UMMZ 130369;
UNL 731

Mainstream, Lower Rio Salado--TNHC 1707, 5795

Rio Sabinas de Coahuila--TNHC 1728, 5932

Rio Sabinas de Nuevo Leon--UNL 439

RIO SAN JUAN SYSTEM

Rio Pilon--UMMZ 162131; UNL 4, 29 616, 643

Rio San Juan and smaller tributaries--UMMZ 97421; UNL 152, 766

Notropis _____NUECES RIVER SYSTEM

Rio Frio--TNHC 5055, 5067; TU 21681, 21709

Nueces River and smaller tributaries--ASU 984, 2837; TNHC 1978 5279;
TU 21555, 22263

Notropis proserpinusDEVIL'S RIVER SYSTEM

Devil's River and smaller tributaries--ASU 1023, 1701, 1716; TNHC
3262, 5670; TU 11910, 24730

PECOS RIVER SYSTEM

Pecos River and tributaries--TNHC 4870; TU 3647, 27949, 36933

BIOGRAPHICAL SKETCH

Glady Lou Lytle was born in Ft. Wayne, Indiana, on November 17, 1942. She received her elementary education in Ft. Wayne, Indiana Public Schools, and in Casa Grande and Eleven Mile Corner Public Schools, Arizona. Her Junior High School education was completed in Jal and Eunice, New Mexico, Public Schools, while her High School Diploma was received from Casa Grande Union High School, Arizona. In 1960, she entered Arizona State University, with honors, and graduated with a Bachelor of Science Degree in Zoology. She began her work, in January 1966, for the Master of Science Degree in Zoology, which she completed in 1972.