



Chromosomes and the Evolution of the Plagopterin Fishes (Cyprinidae) of the Colorado River System

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Source: *Copeia*, Vol. 1973, No. 4 (Dec. 31, 1973), pp. 776-782

Published by: American Society of Ichthyologists and Herpetologists

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Chromosomes and the Evolution of the Plagopterin Fishes (Cyprinidae) of the Colorado River System

TERUYA UYENO AND ROBERT RUSH MILLER

Karyotypes of the five living species (three genera) of the Plagopterini, a monophyletic group of cyprinids restricted to the lower Colorado River basin of Utah, Nevada and Arizona, were investigated to test the nature of variation in chromosome morphology among cyprinid fishes. Results demonstrate that the pattern of chromosomal change is consistent with morphological differences as expressed in a recent systematic revision. Each species has a diploid number of 50. As a group these minnows possess six to nine pairs of metacentric, 12 to 16 pairs of submetacentric-subtelocentric and two to four pairs of acrocentric chromosomes. If the origin of the Plagopterini dates from the Pliocene, our data indicate the amount of chromosomal change that may occur in nature among cyprinids over a period of some six million years or less.

THE greater the diversity of sources of information that are used to assess phyletic relationships the more reliable, and hence more durable, the interpretation is likely to be, assuming appropriate methods of analysis. One new source of data, chromosome number and morphology, has been re-

ceiving increasing attention and shows high promise for interpreting the evolution of fishes. Until about 1965, such investigations were concerned mostly with chromosome number (Post, 1965), but since many fishes have identical numbers this knowledge was of limited value. Practical utilization of fish

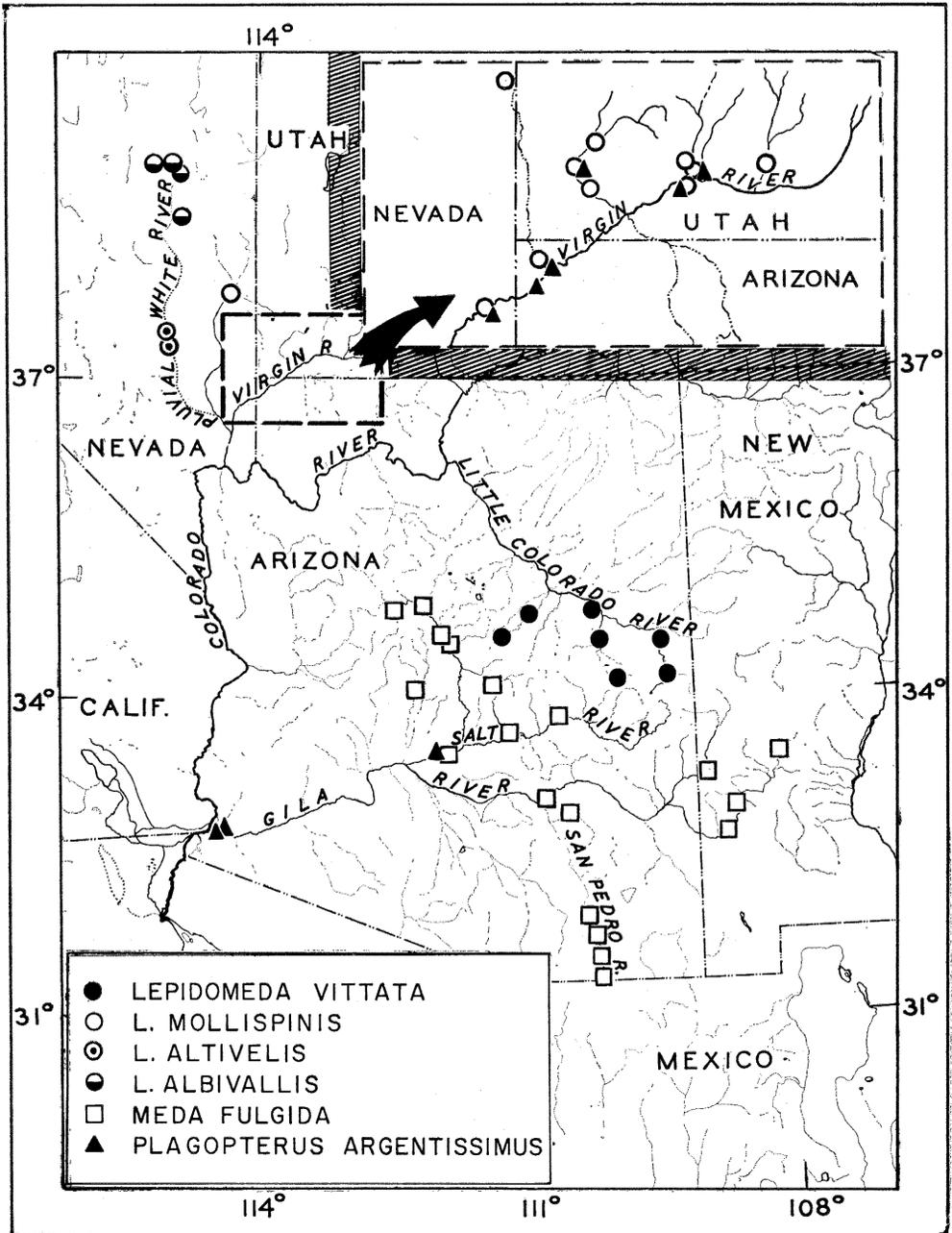


Fig. 1. Distribution of the Plagopterini. Modified after Miller and Hubbs (1960).

karyotypes, involving details of the morphology of the chromosomes themselves, had to await the development of a readily applied technique (McPhail and Jones, 1966). More sophisticated methods, such as the use of

cell-culture techniques, are too inconvenient as yet for general application, but wider use of these important new approaches will come as they are further developed and refined. The systematic application of karyology is

now assured, but it is still too early to know precisely what its value will be for different groups of fishes. Not many studies have appeared that demonstrate a positive correlation between karyotypes and conventional characters (Simon, 1963; Booke, 1968; Chen, 1971; Chen and Ruddle, 1970; Beamish et al., 1971).

In this study chromosome morphology is used to evaluate the interrelationships of some species and genera of cyprinid fishes. To test the method, we chose for analysis an intimately related, compact group of American minnows, the Plagopterini. This tribe includes three genera and six species that are confined to the middle and lower parts of the Colorado River basin in Utah, Nevada, and Arizona (Fig. 1).

The Plagopterini comprise the genera *Lepidomeda*, *Meda* and *Plagopterus*, which are unique among New World cyprinids in possessing spine-like rays in the dorsal and pelvic fins. These specialized ossifications vary from the extreme spine development found in *Meda* and *Plagopterus* to the less modified and variable condition in the species of *Lepidomeda*. The systematics of the group was recently revised by Miller and Hubbs (1960), and a phylogeny was hypothesized on the basis of conventional morphological characters, zoogeography and a consideration of the geological history of the lower Colorado River basin. That revision provided an excellent opportunity to evaluate the systematic value of karyotypes within a small, monophyletic group of minnows.

The results of the chromosome analysis matched remarkably well the interpretation of relationships presented in the systematic revision. Karyotypes are thus seen to be a useful tool for systematic appraisal of the Plagopterini, and it is predictable that they will be of value in other, recently differentiated, cyprinids as well.

MATERIALS AND METHODS

The following specimens were available for study; figures in parentheses are the ranges in standard length for each species. *Lepidomeda albiwallis*: 10 specimens. Six specimens (52 mm–69 mm) from Lund Spring at Lund, White Pine Co., Nevada, R. R. Miller family, 16 August 1969; 4 specimens (62 mm–71 mm) from Preston Big Spring, 3 km NW of Preston, White Pine Co., Nevada, J. E. Deacon, 28 September 1969.

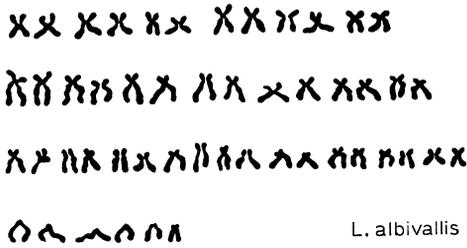
Lepidomeda mollispinis: 4 specimens (34 mm–45 mm) from Beaver Dam Wash above confluence with Virgin River, Mohave Co., Arizona, G. R. and K. B. Smith, 30 July 1969. *Lepidomeda vittata*: 6 specimens (28 mm–60 mm) from Leonard Canyon, tributary to East Clear Creek in Little Colorado River basin, at Dine's Tank (T 13 N, R 12 E), Coconino Co., Arizona, W. L. Minckley, 28 September 1969. *Meda fulgida*: 13 specimens (34 mm–54 mm) from Aravaipa Creek, tributary to San Pedro River, at Wood Ranch, Pinal Co., Arizona, W. L. Minckley, 19 September 1969. *Plagopterus argentsimus*: 5 specimens (23 mm–54 mm) from Virgin River above confluence with Beaver Dam Wash, Mohave Co., Arizona, G. R. and K. B. Smith, 30 July 1969.

Mitotic metaphase chromosome preparations were obtained from gill epithelium using essentially the same method as that described by McPhail and Jones (1966). Specimens were injected with 0.05% Velban and kept alive for two to four hours in well aerated water. A Leitz "Aristophot" and Polaroid Type 57 (ASA 3000) film were used for photography. The optics were 15× ocular and 100× phase contrast oil emulsion objective lens on a Wild M20 microscope. Drawings were made by camera lucida.

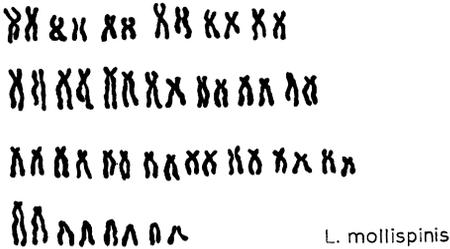
RESULTS

The diploid chromosome number of all species examined in this study is 50. Sex chromosomes were not identifiable. We attempted to classify the chromosomes in three categories, metacentric (m), submetacentric-subtelocentric (sm-st), and acrocentric (t). An attempt was made to distinguish between submetacentric and subtelocentric chromosomes, but these types occur in a continuously graded series and separation proved to be impossible (Figs. 2–3). Cells that showed elongated chromosomes were chosen for study and photography, even though some overlapping occurred, because the position of the centromere was readily seen and this facilitated assignment to one of the three categories.

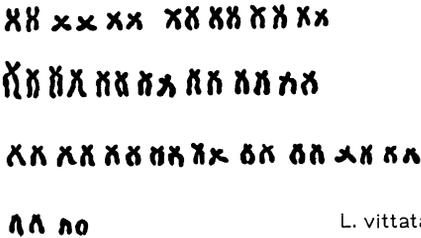
Features that characterize the karyotypes of the Plagopterini are the presence of six to nine pairs of metacentric, 12 to 16 pairs of submetacentric and subtelocentric, and two to four pairs of acrocentric chromosomes. The karyotype of the genus *Lepidomeda* is characterized by the presence of six to seven



L. albivallis



L. mollispinis



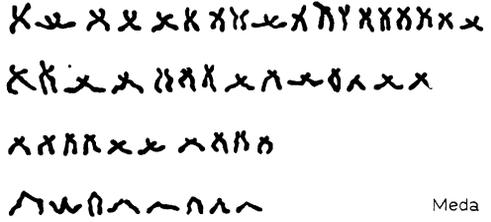
L. vittata

Fig. 2. Camera lucida drawings of the karyotypes of the genus *Lepidomeda*.

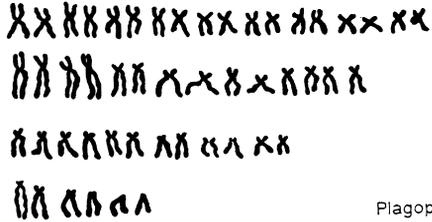
pairs of metacentrics among which three or four pairs closely approach the submetacentric condition. *Meda* and *Plagopterus*, in contrast, have nine pairs of metacentric chromosomes.

Lepidomeda albivallis Miller and Hubbs. The karyotype comprises 6 pairs of metacentric, 16 pairs of submetacentric-subtelocentric and 3 pairs of acrocentric chromosomes. Twenty-five cells were counted.

Lepidomeda mollispinis Miller and Hubbs. The karyotype consists of 6 pairs of metacentric, 15 pairs of submetacentric-subtelocentric and 4 pairs of acrocentric chromosomes. Only 10 cells contained good spreads. In the spread photographed (Fig. 4) the chromosomes were not in the same focal plane and thus focusing was made at an intermediate plane so as to illustrate all of the chromosomes. There was no difficulty,



Meda



Plagopterus

Fig. 3. Camera lucida drawings of the karyotypes of the genera *Meda* and *Plagopterus*.

however, in drawing each chromosome by camera lucida.

Lepidomeda vittata Cope. The karyotype comprises 7 pairs of metacentric, 16 pairs of submetacentric-subtelocentric and 2 pairs of acrocentric chromosomes. Forty-eight cells were counted.

Plagopterus argentissimus Cope. The karyotype comprises 9 pairs of metacentric, 13 pairs of submetacentric-subtelocentric and 3 pairs of acrocentric chromosomes. Twenty cells were counted.

Meda fulgida Girard. The karyotype consists of 9 pairs of metacentric, 12 pairs of submetacentric-subtelocentric and 4 pairs of acrocentric chromosomes. Sixty-six cells were counted.

DISCUSSION

The cyprinid fishes whose karyotypes are reported here include five species which are intimately associated by the development, unique among American minnows, of the ossification and other spinelike modifications of the first two dorsal rays and of the pelvic rays (Miller and Hubbs, 1960: Pl. III). These and other specializations appear only in this group of genera and support the view that the Plagopterini are monophyletic (Miller and Hubbs, 1960).

Among them, *Lepidomeda* has the body covered with scales (somewhat degenerate), but *Meda* is scaleless and *Plagopterus* is virtually so. In *Lepidomeda*, the least modi-

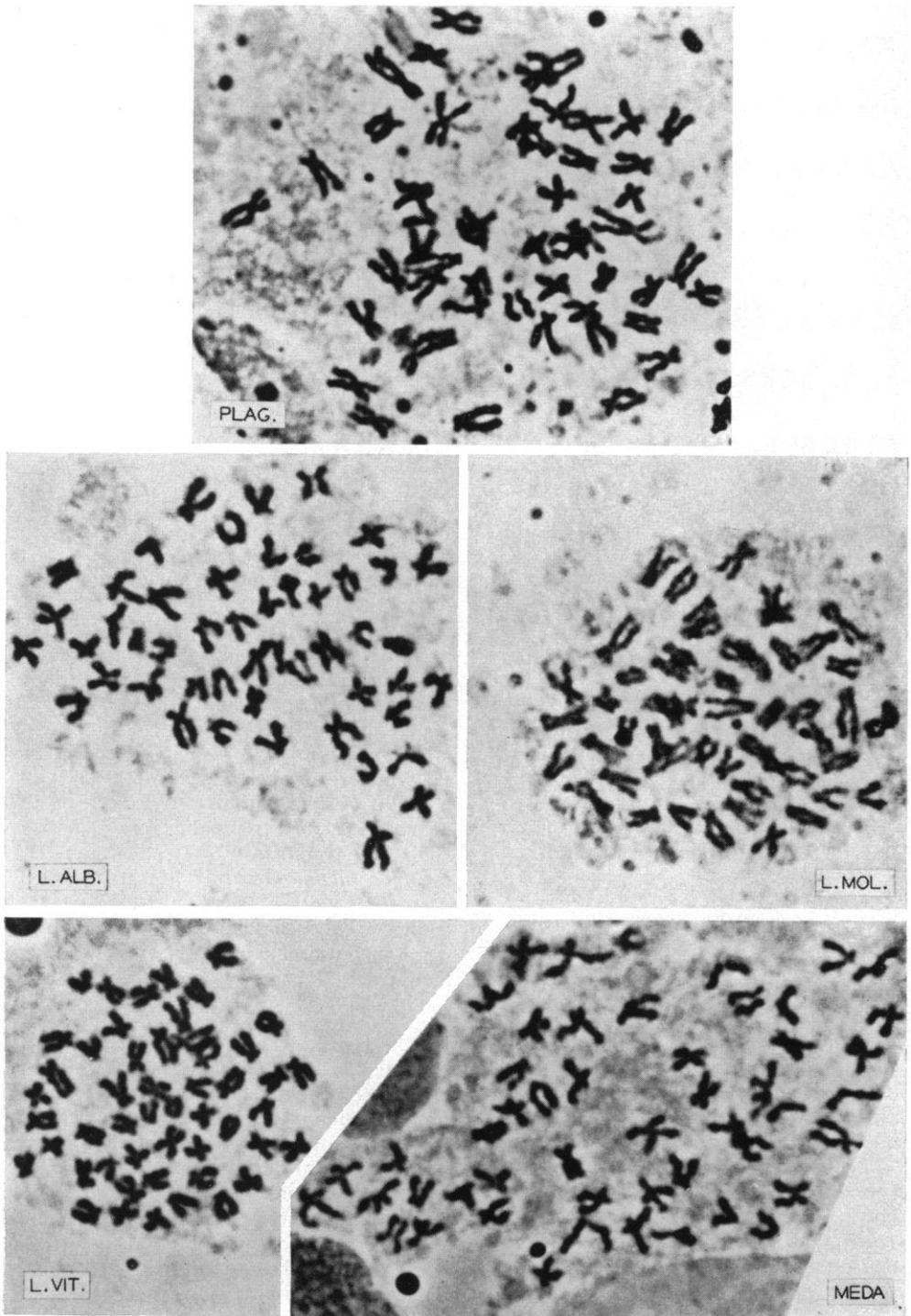


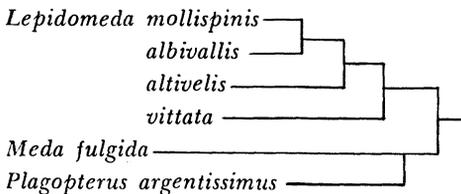
Fig. 4. Chromosomes of the Plagopterini, $\times 2150$. Plag. = *Plagopterus argentissimus*; Meda = *Meda fulgida*; L. alb. = *Lepidomeda albivallis*; L. mol. = *L. mollispinis*; L. vit. = *L. vittata*.

TABLE 1. KARYOTYPIC DIFFERENCES IN THE PLAGOPTERINI. The karyotype of each species, arranged diagonally, is given in the sequence metacentric, submetacentric-subtelocentric, and acrocentric (Levan, et al., 1964).

Taxon	<i>L. alb.</i>	<i>L. mol.</i>	<i>L. vit.</i>	<i>Plagop.</i>	<i>Meda</i>
<i>Lepidomeda albivallis</i>	6-16-3	2	2	6	8
<i>L. mollispinis</i>	2	6-15-4	4	6	6
<i>L. vittata</i>	2	4	7-16-2	6	8
<i>Plagopterus</i>	6	6	6	9-13-3	2
<i>Meda</i>	8	6	8	2	9-12-4

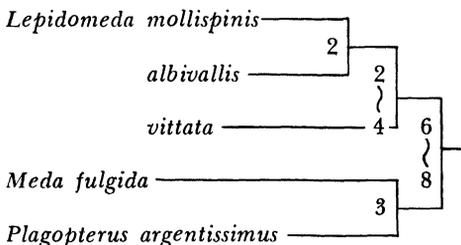
fied plagopterin, the second dorsal spine is longer and stronger than the first, whereas the reverse is true in *Meda* and *Plagopterus*. *Plagopterus* is unique among these genera in having a pair of small barbels. *Lepidomeda* is believed to include the most primitive members of the tribe and hence to represent the ancestral line, whereas *Meda* and *Plagopterus* are each specialized in different ways. All show strong to moderate development of bright silvery coloration on the body.

In the report by Miller and Hubbs (1960), the phenetic relationships of these fishes were expressed in the diagram attached to their analytical key, as follows:



Among the species included above, *L. altivelis* is now believed to be extinct; hence it was unavailable for this study.

If we construct a similar diagram using the total number of different chromosomes in the three categories (m, sm-st, and t), the result is the same as the above diagram, which was based on anatomical traits:



In the second diagram, the numbers indicate the chromosomal difference in karyotypes (see Table 1).

A comparison of the karyotypes of the Plagopterini (Table 1) shows how many chromosomes differ between any two species. Karyotypes of *Lepidomeda* are very similar, with only two to four differences between the three species. *Meda* and *Plagopterus* are more alike than either one is to *Lepidomeda*, having nine rather than six or seven pairs of metacentric chromosomes. This might indicate that *Meda* and *Plagopterus* share a recent common ancestor, and that the deviation from the *Lepidomeda* karyotype was accompanied by an increase in metacentric chromosomes. Matching homologous pairs of chromosomes is difficult, however, except for a few distinctly-shaped ones. But probably selecting homologues will become easier and more accurate in the future, as techniques for determining chromosome markers in fishes (Chen and Ruddle, 1970) become refined.

Lieppman and Hubbs (1969) reported the karyotypes of two American cyprinids, *Notropis lutrensis* (Baird and Girard) and *Notemigonus crysoleucas* (Mitchill), each of which has five or fewer pairs of acrocentric chromosomes. We found also in the Plagopterini and in 40 species among 20 genera of North American cyprinids (unpublished data) that the acrocentric chromosomes constitute less than 20% of the total complement. The other chromosomes approach a continuously graded series from the metacentric to the subtelocentric condition.

Our report provides an example of the type of data for demonstrating the systematic value of karyotypes among closely related species, but we still need more such information in order to understand the relationship

between chromosome morphology and phylogeny in fishes. If the Plagopterini arose sometime during the Pliocene our data indicate how much chromosomal change may occur in nature among cyprinids over a time span of six million years or less. Karyotypes are known to vary in different families of fishes. Consequently, this analysis of cyprinid genera does not necessarily mean that karyotypes will have similar value in other families of fishes. For example, sibling species such as *Fundulus olivaceus* ($2n = 48$) and *F. notatus* ($2n = 40$) (recently referred to *Zygonectes* by Hubbs and Burnside, 1972) may have distinctly different karyotypes (Setzer, 1970) because of Robertsonian fusions, whereas many obviously distinct species in different families or even different orders show virtually identical karyotypes (e.g., some flatfishes, sunfishes and anchovies—Ohno, 1970).

ACKNOWLEDGMENTS

We are very grateful to the following for providing live material: James E. Deacon, W. L. Minckley and Gerald R. Smith. The authorities of the states of Arizona and Nevada kindly issued scientific collecting permits. In the early stages of our work with chromosomes we benefitted from the suggestions of John B. Burch and Charlotte M. Patterson. Elizabeth A. Strauch devoted many tedious hours in selecting spreads to be photographed. Financial support from the National Science Foundation made possible the completion of this work: GB-4854X, GB-6272X and GB-14871, to R. R. Miller, and GB-8212, to The University of Michigan Museum of Zoology for Research in Systematic and Evolutionary Biology.

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