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Cytogenetic Studies in North American Minnows (Cyprinidae) I. Karyology of Nine California Genera

J. R. Gold and J. C. Avise

Karyotypes of nine species representing nine genera of cyprinid fishes inhabiting California were examined. The nine genera, including *Hesperoleucus, Lavinia, Mylopharodon, Pogonichthys, Ptychocheilus, Orthodon, Richardsonius, Gila* and *Notemigonus*, all have diploid chromosome numbers of 50. *Notemigonus* is the only genus non-native to California, having been introduced from the eastern United States. Measurements of centromeric indices suggested differences in fundamental arm number among the genera. In addition, one long chromosome with a distally located centromere was observed in the karyotype of each species, and may be of future use in North American cyprinid systematics.

THE cyprinid fishes endemic to the North American continent include a vast array of different forms thought to belong (with a single possible exception) to one subfamily, the Leuciscinae (Miller, 1959). It is generally believed that most North American cyprinids are of relatively recent phyletic origin and may share a common ancestry stemming from a few cyprinid fishes which migrated from Eurasia during the Miocene (Miller, 1959, 1965).

Recently, Avise et al. (1975) and Avise and Ayala (1976) reported studies on biochemical-genetic differentiation among nine genera of cyprinid fishes inhabiting California. Their results suggested that four genera were similar in genic content and were perhaps of monophyletic origin. The remaining five genera were less closely related genically, and may represent the mean levels of genic divergence between all North American cyprinids.

In the present study, we have examined the karyotypes of the nine taxa studied by Avise and Ayala (1976). Our results indicate that all nine genera (including one genus native to the eastern United States and possibly a member of a different subfamily, the Abramidinae) are

TABLE 1. DISTRIBUTION OF CHROMOSOME NUMBER COUNTS FROM KIDNEY CELLS OF INDIVIDUALS, AND CHROMOSOME ARM NUMBER ESTIMATES FROM MODAL KARYOTYPES OF NINE SPECIES (GENERA) OF NORTH AMERICAN CYPRINIDS.

Taxon	# Individuals Sampled	# of cells with 2n =					Total # cells	# chromosomes with median or submedian centromeres	# chromosomes with subterminal or terminal centromeres	Fundamental chromosome arm number
		≤48	49	50	51	≥52				
Hesperoleucus symmetricus	(8)	10	13	75	1	–	99	42	8	92
Lavinia exilicauda	(3)	18	3	54	–	–	75	42	8	92
Ptychocheilus grandis	(3)	7	7	48	2	–	64	42	8	92
Mylopharodon conocephalus	(3)	15	8	57	–	–	80	44	6	94
Pogonichthys macrolepidotus	(2)	14	10	72	3	–	99	44	6	94
Orthodon microlepidotus	(2)	4	9	44	2	1	60	44	6	94
Notemigonus crysoleucas	(5)	7	8	59	–	–	74	44	6	94
Gila bicolor	(4)	17	12	106	–	–	135	44	6	94
Richardsonius egregius	(5)	10	18	66	6	–	100	36	14	86

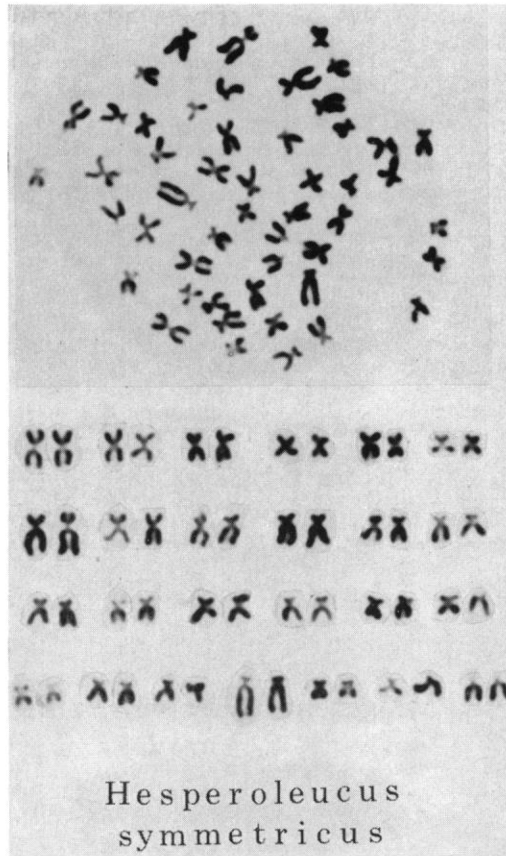

Fig. 1. Somatic metaphase chromosomes (from kidney) of *Hesperoleucus symmetricus* ($2n = 50$).

karyotypically similar. One long chromosome with a distally located centromere was observed in the karyotype of each genus and may potentially be of use in North American cyprinid systematics.

MATERIALS AND METHODS

All specimens were collected either by seining or by angling, and were brought live to the Fisheries Biology Research Facility at the University of California at Davis campus. The nine species (collection sites) were as follows: *Hesperoleucus symmetricus*, *Lavinia exilicauda* and *Ptychocheilus grandis* (Russian R., Mendocino Co.); *Mylopharodon conocephalus* (Chowchilla R., Madera Co.); *Pogonichthys macrolepidotus* (Sacramento R., Sacramento Co.); *Orthodon microlepidotus* (Clear L., Lake Co.); *Richardsonius egregius* (Sagehen Cr., Placer

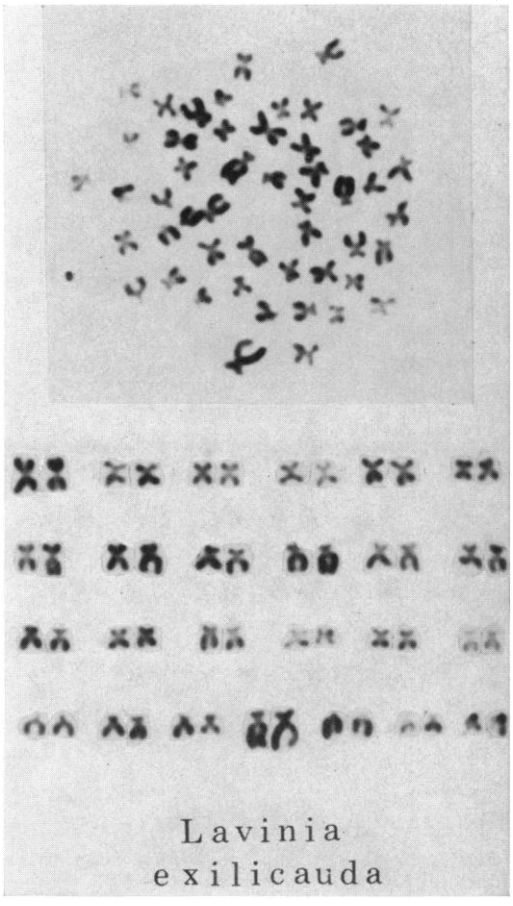

Fig. 2. Somatic metaphase chromosomes (from kidney) of *Lavinia exilicauda* ($2n = 50$).

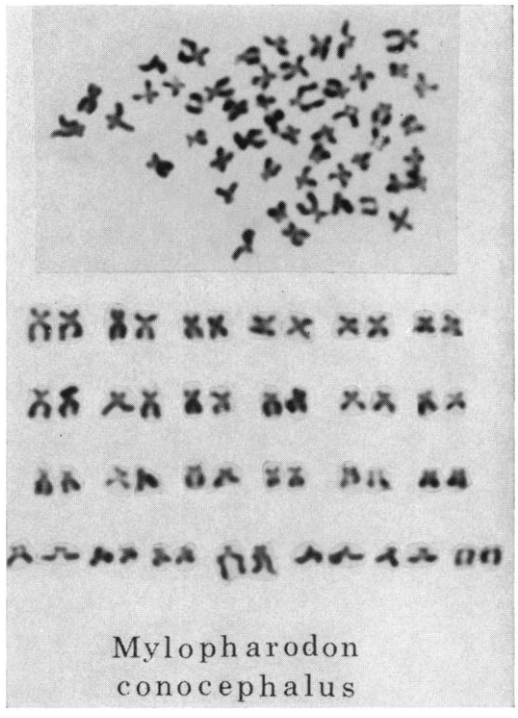

Fig. 3. Somatic metaphase chromosomes (from kidney) of *Mylopharodon conocephalus* ($2n = 50$).

Co.); *Gila bicolor* (Crowley L., Mono Co.); and *Notemigonus crysoleucas* (Bass L., Madera Co.).

The method of chromosome preparation employed was as outlined in Gold (1974). Only well-spread metaphases were selected for study, and were photographed using high contrast film. Chromosome counts were made separately by both investigators, and were considered as accurate only when complete agreement was reached.

Results

Karyology of the species.—The distributions of chromosome number counts from each of the nine species (genera) are shown in Table 1. Usually, at least 10 cells were examined from each individual specimen. Sharp and consistent modes of $2n = 50$ chromosomes (between 66–80% of counts) were observed for all nine genera. These chromosome numbers are consistent with the unpublished work of Uyeno, who has found that some 60 species in 26 genera of North American Cyprinidae have chromosome numbers of $2n = 50$ (Uyeno, 1971). The chromosome numbers of *Notemigonus* (*crysoleucas*), *Hesperoleucus* (*symmetricus*), *Gila* (*orcutti*) and *Ptychocheilus* (*lucius*) have been published previously, and were the same as found here (Lieppman and Hubbs, 1969; Uyeno and Smith, 1972; Greenfield and Greenfield, 1972).

No aneuploidy or intra- or interindividual polymorphism was observed as in other teleostean species (Roberts, 1970; Davisson et al., 1972, 1973; Ross, 1973; Gold and Gall, 1975). The overwhelming majority of nonmodal counts were hypomodal ($2n < 50$), and probably stemmed from chromosome loss during preparation or counting errors. The total number (over all species) of hypermodal counts ($2n > 50$) was less than 2% of all counts and can be accounted for by chromosome breakage, premature chromatid separation, or counting errors.

Karyograms of each species were prepared

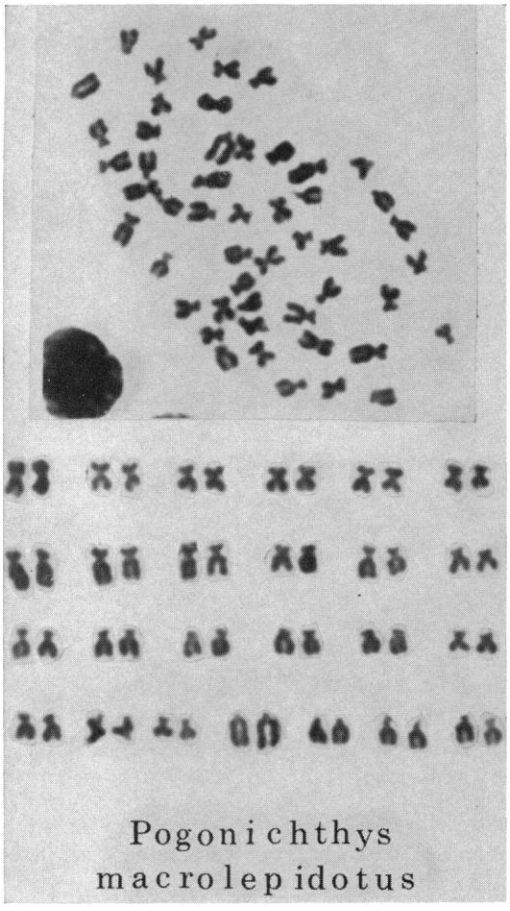

Fig. 4. Somatic metaphase chromosomes (from kidney) of *Pogonichthys macrolepidotus* ($2n = 50$).

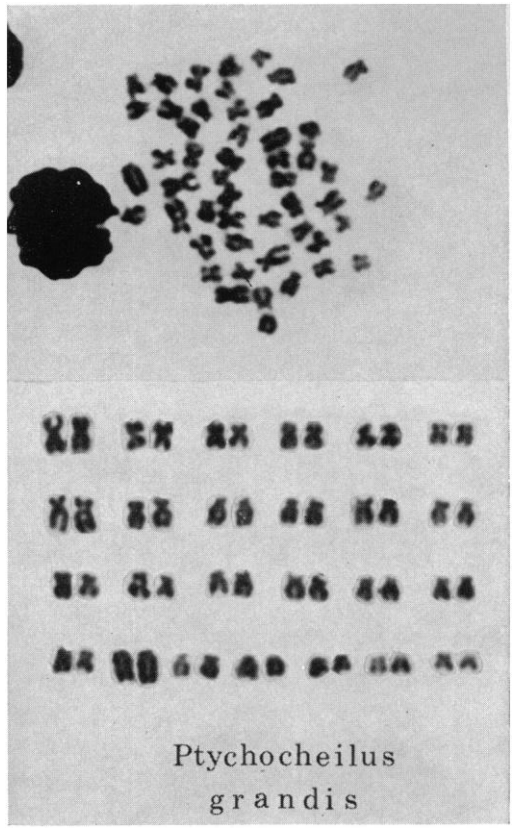

Fig. 5. Somatic metaphase chromosomes (from kidney) of *Ptychocheilus grandis* ($2n = 50$).

from the best-spread cells having modal counts, and are presented in Figs. 1–9. The apparently asymmetrical karyotypes (White, 1973) of the nine cyprinid genera examined is notably different from the symmetrical karyotypes (where all chromosomes are approximately similar morphologically) exhibited by several diverse orders of teleostean fishes (Ohno, 1974).

Karyotypic differentiation between species.— The finding that all nine species (genera) have chromosome numbers of $2n = 50$ suggests that chromosomal changes involved in or associated with speciation in these fishes probably did not include rearrangements in chromosome number, i.e., Robertsonian fusion or dissociation. However, the variations in chromosome size and shape apparent in the karyotypes of each species suggest that other chromosomal rearrangements, e.g. centromeric shifts, which do not alter chromosome number (Ohno et al., 1966) might have occurred during the evolution of each species. Fundamental arm number determinations were carried out on representative karyograms of each species to examine this possibility. Measurements of relative chromosome arm lengths were made using precision calipers, and each homologous chromosome pair was scored by its centromeric index, i.e., median, submedian, subterminal or terminal (after Levan et al., 1964). The fundamental arm number for each species was estimated by scoring chromosomes with median or submedian centromeres as biarmed, and chromosomes with subterminal or terminal centromeres as uniarmed. The estimates of fundamental arm number (Table 1) reveal three groupings. *Mylopharodon, Pogonichthys, Orthodon, Notemigonus* and *Gila* comprise one group with 94 arms; *Hesperoleucus,*

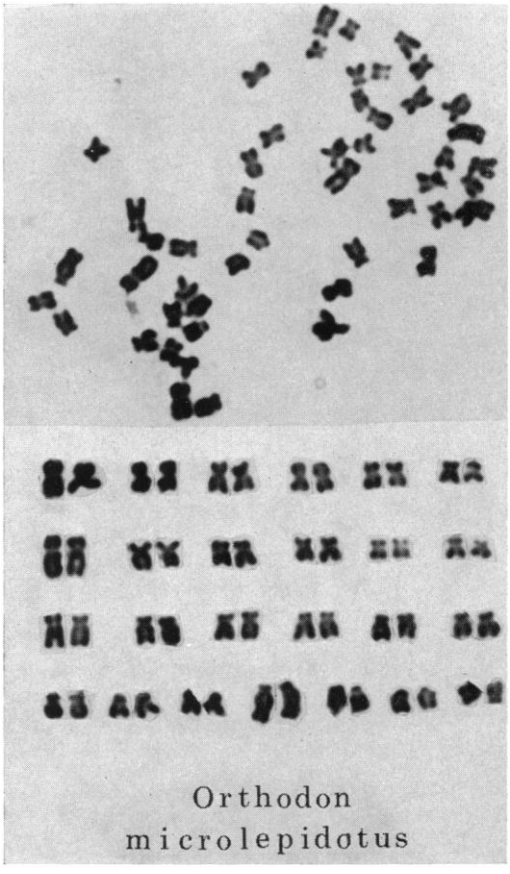

Fig. 6. Somatic metaphase chromosomes (from kidney) of *Orthodon microlepidotus* ($2n = 50$).

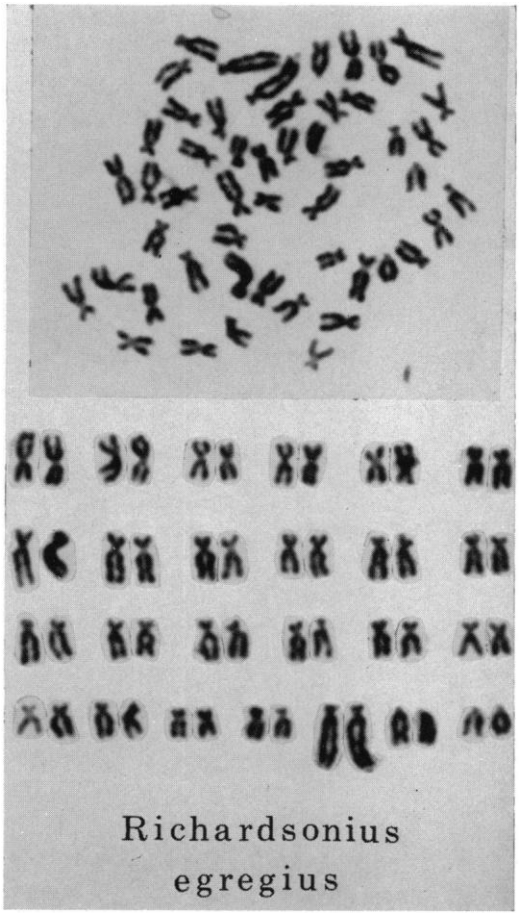

Fig. 7. Somatic metaphase chromosomes (from kidney) of *Richardsonius egregius* ($2n = 50$).

Lavinia and *Ptychocheilus* a second with 92 arms; and *Richardsonius* a third with 86 arms.

In our opinion the data on arm number must be considered with reservation, as neither of us is entirely confident of the reliability of chromosome morphometric data. Depending on the degree of arm attenuation, arm length ratios will vary for a particular homologous pair, and furthermore, even the matching of homologous pairs is at best partially subjective. Many chromosomes are morphologically similar. In our judgement, a conservative interpretation of the data is warranted, and the karyotypes of the nine cyprinid genera examined here are best considered as very similar, but not identical.

An attempt also was made to determine if differences in relative chromosome lengths exist between species pairs. From the morphometric measurements obtained in the estimates of centromere position, no significant differences in relative chromosome lengths were apparent among the nine species. Generally, the chromosomes varied in each species from ca. 4–8 microns.

One further cytological observation bears mention. In previous chromosome studies of the North American cyprinids, several authors noted the presence or absence of a long chromosome with a sub-median to terminally located centromere. Such a chromosome invariably was observed in all cells of each cyprinid species examined here. The presence or absence of this chromosome (and its centromeric index) for most of the North American cyprinid karyotypes published to date is shown in Table 2. In four of the 18 species examined, this chromosome

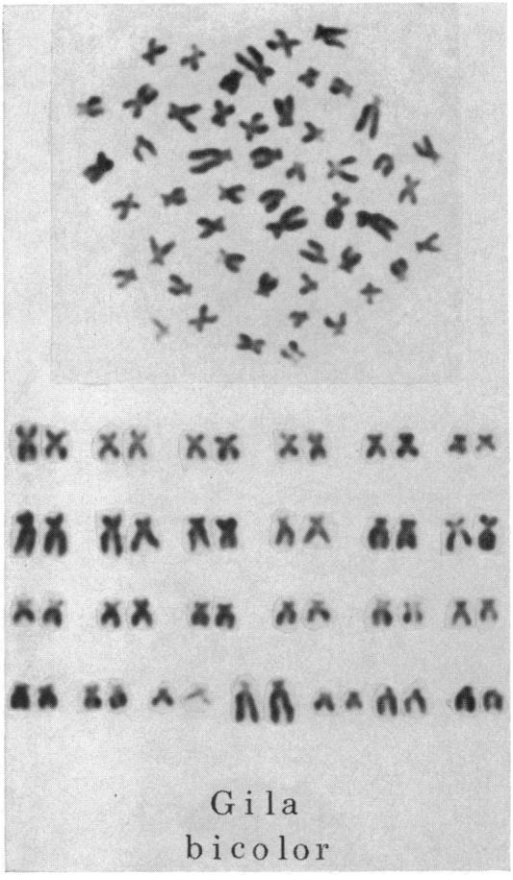

Fig. 8. Somatic metaphase chromosomes (from kidney) of *Gila bicolor* ($2n = 50$).

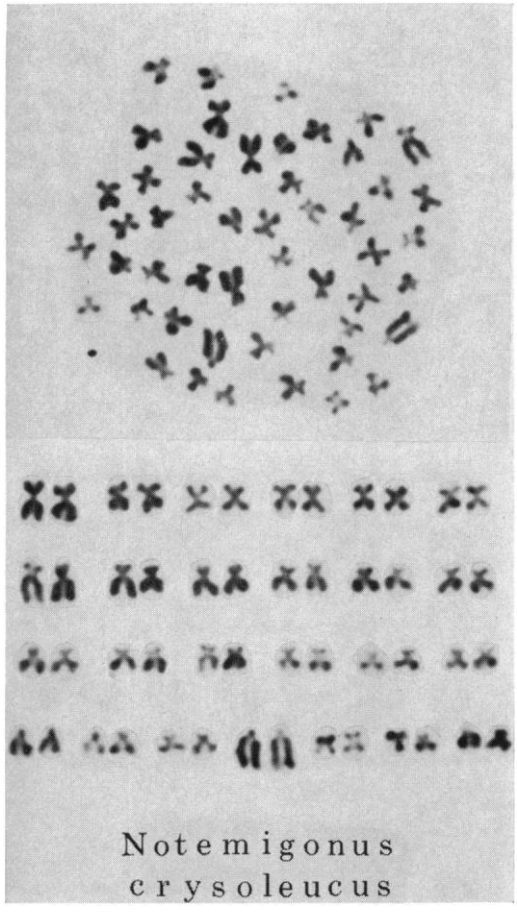

Fig. 9. Somatic metaphase chromosomes (from kidney) of *Notemigonus crysoleucas* ($2n = 50$).

was not readily discernable. In the remaining 14 the chromosome is identifiable, and there apparently exists some variation in centromere position. Possibly, this chromosome may be of future use in North American cyprinid systematics. However, it needs to be shown that the chromosome is homologous across species before such considerations can be made.

Discussion

The present study has revealed that all nine cyprinid genera examined have identical chromosome numbers of $2n = 50$. Of the nine, eight are New World genera endemic to the western United States. *Notemigonus* was introduced to California from the eastern United States, and may be the only North American member of the Old World subfamily Abramidinae (Miller, 1959). Karyotypically, *Notemigonus* appears to be the same as the other genera examined.

To date, all but two of the North American cyprinids karyotyped have diploid chromosome numbers of 50 (McPhail and Jones, 1966; Denton and Howell, 1969; Lieppman and Hubbs, 1969; Uyeno, 1971; Greenfield and Greenfield, 1972; Campos and Hubbs, 1973; Denton, 1973; Greenfield et al., 1973; Uyeno and Miller, 1973; Avise and Gold, 1977). The monotypic genus *Hemitremia* with 52 chromosomes (R. R. Miller, pers. comm.) and *Opsopoeodus* (= *Notropis*) *emiliae* with 48 chromosomes (Campos and Hubbs, 1973) are the exceptions. This is not the case in the Old World (Eurasian) cyprinids. Reported chromosome numbers in diploid species range from 44 to 104, although most species fall in the range from

TABLE 2. CENTROMERIC INDICES OF THE LONG CHROMOSOME WITH A SUB-MEDIAN TO TERMINALLY LOCATED CENTROMERE IN THE KARYOTYPES OF NORTH AMERICAN CYPRINIDS.

Taxon	Chromosome Distinguishable	Centromeric Index †	Source
Rhinichthys evermanni	No	—*	McPhail and Jones (1966)
Notropis stilbius	Yes	submetacentric*	Denton and Howell (1969)
Notropis callistius	Yes	submetacentric*	Denton and Howell (1969)
Notropis venustus	Yes	submetacentric	Campos and Hubbs (1973)
Notropis texanus	No	—	Campos and Hubbs (1973)
Opsopoeodus emiliae	No	—	Campos and Hubbs (1973)
Notropis lutrensis	No	—	Lieppman and Hubbs (1969)
Notemigonus crysoleucas	Yes	telocentric	Lieppman and Hubbs (1969)
Notropis cornutus	Yes	submetacentric	Greenfield et al. (1973)
Chrosomus erythrogaster	Yes	acrocentric	Greenfield et al. (1973)
Lavinia exilicauda	Yes	submedian to subterminal	This paper
Hesperoleucus symmetricus	Yes	subterminal	This paper
Richardsonius egregius	Yes	subterminal	This paper
Orthodon microlepidotus	Yes	subterminal	This paper
Mylopharodon conocephalus	Yes	subterminal	This paper
Gila bicolor	Yes	subterminal	This paper
Notemigonus crysoleucas	Yes	subterminal	This paper
Ptychocheilus grandis	Yes	subterminal to terminal	This paper
Pogonichthys macrolepidotus	Yes	terminal	This paper

† Centromeric indices are either as scored by the authors, or as estimated by us from published karyograms.
* Our estimates of centromeric indices.

48 to 52 (Chiarelli and Capanna, 1973; Denton, 1973; Park, 1974).

Miller (1959, 1965) supported the premise that most North American cyprinids are of recent origin (Miocene), and may stem from a single or few Asian ancestors. The similarity in chromosome number among the New World cyprinids does suggest a recent origin, at least in view of the variation in chromosome number among the older Eurasian species. The ancestry of New World cyprinids, however, cannot be ascertained solely on karyological grounds. A close morphological relationship between the Old World genus *Abramis* and *Notemigonus* is well documented (Berg, 1949; Miller, 1959); and Lieppman and Hubbs (1969) suggested from morphological and karytotypic evidence that either *Scardinus erythrophthalmus* or *Abramis brama* could have been ancestral to New World cyprinids. Their observations of karyotypic similarities, however, were based on Post's (1965) report that both *Scardinus* and *Abramis* had $2n = 52$ chromosomes. Wolf et al. (1969) subsequently reported that *Abramis* had 50 chromosomes; and Chiarelli et al. (1969) and Ohno (1974) published karyograms of *Scardinus* showing 48 chromosomes. Thus, *Abramis* would appear a logical choice as a progenitor of the New World cyprinids; but a firmer conclusion must await more detailed analyses.

Our morphometric measurements of chromosome arm lengths indicated differences in fundamental arm numbers among the nine genera. *Richardsonius* was scored as having the fewest arms (86); *Lavinia, Hesperoleucus* and *Ptychocheilus* formed a second group having 92 arms; and *Orthodon, Mylopharodon, Pogonichthys, Gila* and *Notemigonus* comprised the largest group having 94 arms. Changes in arm number, but not chromosome number, generally imply uneven pericentric inversions or translocations (Ohno et al., 1966). Cytogenetic events of this sort may have played a significant role in the divergence and speciation of the North American cyprinids. But until more definitive chromosome staining methods (which could better identify particular chromosomes) are employed, we think it safest not to place much emphasis on the apparent differences in fundamental arm number.

The long chromosome with a distally located centromere may be of significance in the system-

atics of the North American cyprinids. This chromosome was observed in the karyotype of each genus examined, and has been reported in the karyotypes of other North American cyprinids. The centromeric index of this chromosome as well as its presence or absence, apparently differs from taxon to taxon, and may indicate different phyletic lines. It remains to be seen if this chromosome is homologous across all species, and if the centromeric index measurements are reliable.

Acknowledgments

The authors thank G. A. E. Gall of the Animal Science Department at the University of California at Davis, in whose laboratory this project was carried out. We also thank John and Mitzi McDonald, Bill Emery, Peggy Lehman, Randy Smith and Terry Mills for assisting in the field work. We especially thank G. E. Bradford, Chairman of the Animal Science Department at UC Davis, for providing departmental funds to have the karyograms photographed. The work was partially supported by Dingell-Johnson Project California F-28-R, "Trout Genetics" and by AEC contract AT (04-3) 34.

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Genetic Uniformity Throughout the Range of the Hellbender, *Cryptobranchus alleganiensis*

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Genetic varation was analyzed in populations of the paedogenic salamander *Cryptobranchus alleganiensis* throughout its range. An exceptionally high degree of homozygosity was observed at 24 genetic loci with most populations monomorphic at all loci. No major geographical variation was observed throughout the range of this species despite the fact that it occurs in a number of isolated drainage systems.

THE salamander family Cryptobranchidae is extant in parts of Japan, China and eastern North America. It is comprised of only two genera. *Andrias* is represented by one living species in Asia, but is known from fossils dating from the Oligocene of Europe and the Miocene of North America. *Cryptobranchus* also consists of one living species occurring in a number of isolated drainages in eastern North America. Its fossil history is unknown. Cryptobranchids are considered among the most primitive of salamanders, and appear to have been morphologically conservative throughout their evolutionary history (Meszoely, 1966).

Two subspecies of *Cryptobranchus alleganiensis* are currently recognized: *alleganiensis* occurring in portions of the Susquehanna, Ohio and Missouri river drainages and *bishopi* in portions of the Black River system in southern Missouri and northern Arkansas. Populations referrable to *bishopi* are characterized by rather minor criteria including smaller spiracle size, increased chin blotching, smooth lateral line system in the pectoral region and dorsal blotching as opposed to the spotting usually present in *C. a. alleganiensis* (Nickerson and Mays, 1973). These populations in the past have been assigned specific status, though only subspecific rank is currently accepted (Dundee, 1971). Isolation in a number of drainages has precluded the possibility of natural hybridization, and artificial crosses have not been made.

Several workers have recently attempted to examine differences between the two races of *C. alleganiensis*. Wortham (1970) noted minor differences in a serum protein component of the two races. Jerrett and Mays (1973) compared a number of hematological parameters in both forms. Melton (pers. comm.) observed a difference in DNA content associated with red blood cell size in his comparison of the two taxa.

The present study utilized electrophoretic techniques to examine relationships of the two races of *C. alleganiensis*, as well as to observe the effect, if any, that isolation in a number of drainages has had on the genetic composition of this species.

MATERIALS AND METHODS

A total of 137 specimens of *C. alleganiensis* were used in this study. Specimens were collected from populations in each of the major drainage systems in which this species occurs