THE UNIVERSITY OF MANITOBA

KARYOTYPIC ANALYSIS OF THE SOMATIC CHROMOSOMES OF NOTURUS GYRINUS (MITCHILL)(ICTALURIDAE: TELEOSTEI)

by

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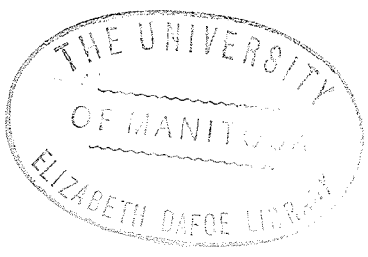

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ABSTRACT. A statistical study of the metaphase chromosomes of the North American catfish, Noturus gyrinus (Mitchill) (tadpole madtom), has shown that nine homolog groups can be identified among the 42 somatic chromosomes of this species. Relative length measurements of chromosomal arms on a cellular base (RLC) and on a group base (RLG) formed the basic data from which coordinate karyograms were constructed. Three median (M-1, M-2 and M-3), four submedian (SM-1, SM-2, SM-3 and SM-4), and two subterminal (ST-1 and ST-2) homolog groups were identified between arm ratio isopleths 1.0-1.7, 1.7-3.0, and 3.0-7.0, respectively. No terminal chromosomes were identified between arm ratio isopleth 7.0 and ∞ , nor was sexual heterogamety evident. The N. gyrinus karyotype was compared with three other known catfish karyotypes: Clarius batrachus (Clariidae), Hypostomus plecostomus (Loricaridae), and Ictalurus punctatus (Ictaluridae). Only M-1 and M-2 homolog groups appeared common to all four karyotypes. Comparison of homolog groups suggests that the loricarid and ictalurid karyotypes have undergone extensive chromosomal reorganization by means of pericentric inversion while the clariid karyotype appears to have remained relatively unmodified from an ancestral form possessing 52-56 telocentric chromosomes.

INTRODUCTION

Of the 413 families of teleosts listed by Greenwood et al. (1966), 192 species representing only 35 families and 11 orders of teleostean vertebrates have chromosome data for one or more species. Indeed, so few species have been examined karyologically that little can be

concluded regarding the probable derivation of their chromosome complements. Most cytogenetic knowledge applicable to systematic problems is derived from the studies of remarkably few workers who have concentrated on the following five fish families: Salmonidae, including Coregoninae and Thymallinae, (Svardson 1942, 1945, 1958; Kupka, 1948; Boothroyd, 1959; Nogusa, 1960; Simon, 1963; Simon and Dollar, 1963; Rees, 1964, 1967; Karbe, 1964; Ohno et al., 1965, 1967b; Booke, 1968; Roberts, 1970); Cyprinidae (Nogusa, 1960; Post, 1965; Ohno and Atkin, 1966; Ohno et al., 1967a; Muramoto et al., 1968; Wolf et al., 1969); Cyprinodontidae (Scheel, 1966a, 1966b, 1968; Setzer, 1968, 1970; Chen 1970, 1971; Chen and Ruddle, 1970); Poeciliidae (Friedman and Gordon, 1934; Wickbom, 1941, 1943; Ohno and Atkin, 1966; Schultz, 1967; Schultz and Kallman, 1968); Centrachidae (Roberts, 1964; Becak et al., 1966; Ohno and Atkin, 1966).

In these families and very recently in Gasterosteidae (Chen and Reisman, 1970), adequate cytogenetic data is now available to begin to infer phylogenetic relationships among species on the basis of comparative chromosome morphology. (Chen, 1971; Ohno 1970a, 1970b.) Correlated cytogenetic studies of relative DNA content and electrophoretic analysis of tissue protein components have further elucidated systematic relationships among lower chordates. (Ohno and Atkin, 1966; Taylor, 1966; Atkin and Ohno, 1967; Ohno et al., 1967a, 1967b; Bender and Ohno, 1968; Booke, 1968; Klose et al., 1968; Muramoto et al., 1968; Wolf et al., 1969; Behnke, 1970). Ohno (1970b) provides a detailed discussion of this subject.

The catfishes (Siluriformes) are among those orders of fishes which have received little attention cytogenetically. Nogusa (1960)

reports diploid counts of 58 rod-shaped (acrocentric) chromosomes for Parasilurus asotus (Siluridae) (n = 29) and 56 rod-shaped chromosomes for Pelteobagrus nudiceps (Bagridae) (n = 28) but adequate material was not provided for karyological analysis of these two species. Somatic chromosome data are available, however, for a single species in three other catfish families: Clarius batrachus (Clariidae), the walking catfish, having 2n = 52 (Srivastava & Das, 1968); Hypostomus plecostomus (Loricaridae), the armoured catfish, having 2n = 54 and Ictalurus punctatus (Ictaluridae), the channel catfish, having 2n = 56 (Muramoto et al., 1968). The chromosomes of these three species have been karyotyped according to conventional methods which sorts the chromosomes into metacentric-submetacentric, subtelocentric and acrocentric (telocentric) categories by inspection. Accordingly, C. batrachus is reported to have 6 metacentrics and 46 acrocentrics, while H. plecostomus and I. punctatus have karyotypic formulas of 24msm + 12st + 18t and 16msm + 22st + 18t, respectively.

The purpose of this particular study is, first, to determine the diploid number and morphological characteristics of the chromosomes of a second species of Ictalurid, Noturus gyrinus (Mitchill) (tadpole madtom) and, secondly, to examine patterns of chromosomal morphology among known catfish karyotypes that would suggest possible derivation of their chromosome complements.

METHODS

Chromosome preparations were made from gill filament epithelial cells of actively-growing juvenile specimens following the method used by Stewart and Levin (1968) to obtain permanent dry mounted smears of

mitotic chromosomes. Fish, approximately 4.5 cm in body length (Fig. 1C), were given a dorsal intermuscular injection of 0.05-0.10 ml of 0.01% colchicine solution using a 27-gauge needle and tuberculin syringe. In small specimens, approximately 3.0 cm in body length (Fig. 1D), a portion of the injection was administered intraperitoneally. Injected specimens were placed in a well-aerated tank 2-6hrs. at 16-20°C. The fish were killed by pithing and the fourth branchial arch removed and placed in fish Ringer's. Mucous, blood and debris were carefully removed from the gill lamellae. Cleaned arches were transfered to 0.1 M potassium cyanide (KCN) for 30-90 sec, depending on the size of the arch, then transfered to triple glass-distilled water for a 3-5 min dialysis period. When the filaments were visibly swollen, the arch was transfered to 45% acetic acid fixative for at least 15 min. Following fixation, a monolayer of cells was prepared by "painting" the tips of the gill filaments across a pre-cleaned glass microscope slide (Esco: 1mm thickness). The smear was allowed to air-dry and then stained in Giemsa's stain. The stained slides were rinsed in distilled water and allowed to air dry after which they were mounted with Permount mounting medium and a #0 Corning cover-glass.

All slides were examined for intact, flattened and well-spread metaphase chromosome complements. Suitable chromosome spreads were photographed under 100X oil-immersion planapochromat lens at a photomagnification of 630X. Parametric measurements were made from ca2800X photographic enlargements.

Individual nuclei were karyotyped by attaching double-stick tape to the back of photographic enlargements, cutting out the individual

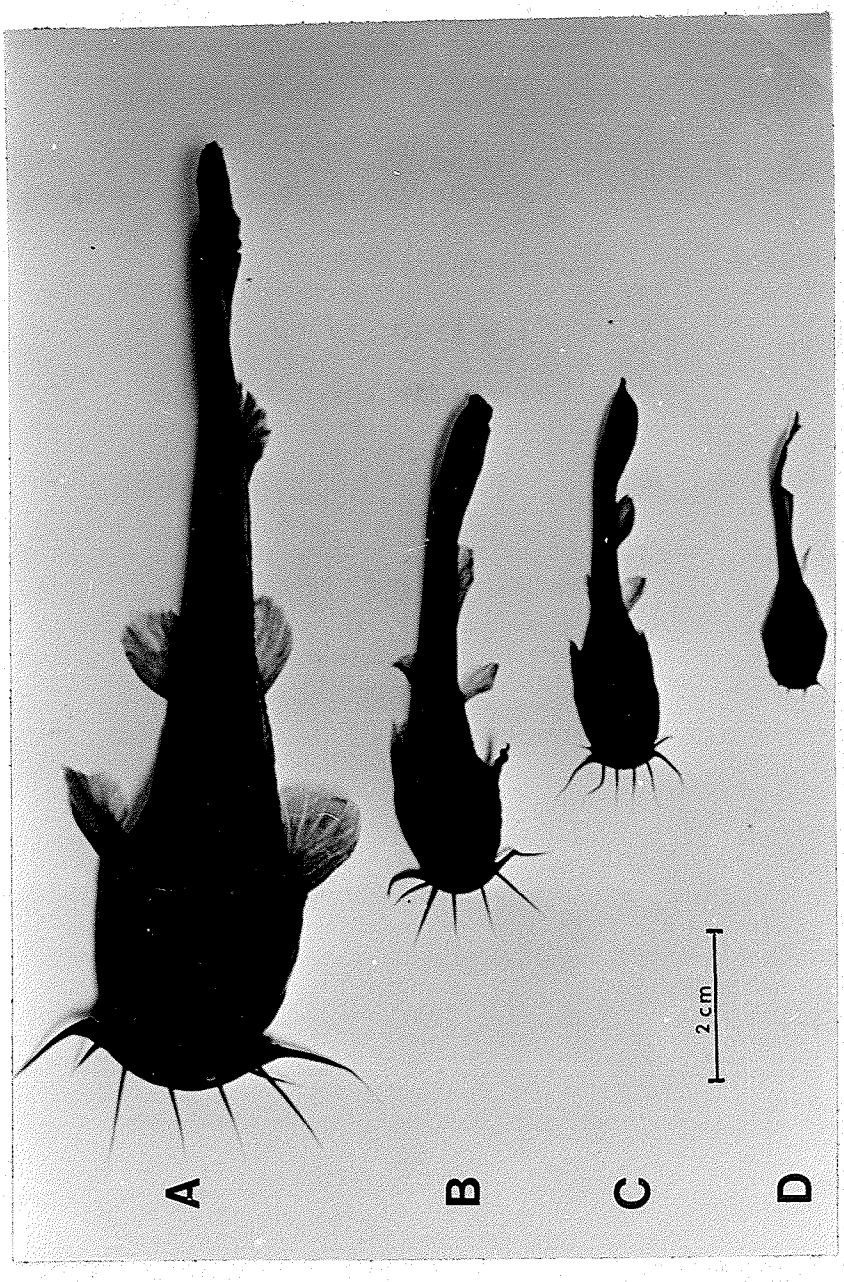
Figure 1 A-D. Total body length variation in Noturus gyrinus specimens used in this study.

A. Mature adult, 12.7cm.

B. Mature adult, 6.7cm.

C. Large juvenile, 5.4cm.

D. Small juvenile, 3.8cm.


A
B
C
D
2 cm

chromosomes and temporarily affixing them to a piece of wire or synthetic screening. The screen facilitated manipulation of chromosomes during inspection analysis. Chromosomes were tentatively assigned to a homolog or homolog group on the basis of over-all length and position of centromere. Each chromosome was then quantitatively described by measuring the length of every chromatid arm with a divider and expressing the measure in arbitrary units with the use of a finely divided rule as described by Ruddle (1964). Further classification of chromosome groups was based on the arm ratio (long arm/short arm) nomenclature of Levan et al.(1964) which can be summarized as follows:

Term	Centromeric position	Arm ratio	Chromosome designation
M	median sensu stricto	1.0	metacentric
m	median region	1.0 - 1.7	metacentric
sm	submedian region	1.7 - 3.0	submetacentric
st	subterminal region	3.0 - 7.0	subtelocentric
t	terminal region	7.0 - ∞	telocentric
T	terminal sensu stricto	∞	telocentric

Length measurements of chromosomal arms form the basic data for karyotypic analysis. Ruddle (1964) has provided the rationale for the notation and formulae employed here. The length of the long arm (l) together with that of the short arm (s) describes the over-all length of the chromosome (c) such that: $c = l + s$. The centromeric position or arm ratio (AR) is described by the length of the long arm relative to that of the short arm such that: $AR = l / s$. A single value for the long or short arm can be obtained by averaging the length of the sister chromatid arms. This value may be expressed in two forms:

(a) absolute measurement (AL) in arbitrary units and (b) relative or percentage measurements. The measurements represented by RLC (relative length on a cellular base) describes the arm length as a decimal or percentage of the combined lengths of all the chromosomes in the cell. The sum of the RLC measurements is here termed the genome length. The measurement represented by RLG (relative length on a group base) compares a particular arm on a decimal or percentage basis with the total chromosomal length of the particular restricted group of chromosomes to which the chromosome in question belongs. The sum of the RLG measurements is here termed the group length.

The notations and relationships to these systems of length representations have been adapted from Ruddle (1964) for N. gyrinus chromosomes as follows:

$$ {}^{1}RLC\sigma(i) = \frac{{}^{1}AL\sigma(i)}{\sum_{i=1}^{42} {}^{1}AL\sigma(i) + \sum_{i=1}^{42} {}^{s}AL\sigma(i)} $$

$$ {}^{s}RLC\varphi(i) = \frac{{}^{s}AL\varphi(i)}{\sum_{i=1}^{42} {}^{1}AL\varphi(i) + \sum_{i=1}^{42} {}^{s}AL\varphi(i)} $$

$$ {}^{s}RLG\sigma(i) = \frac{{}^{s}AL\sigma(i)}{\sum_{i=1}^{4} {}^{1}AL\sigma(i) + \sum_{i=1}^{4} {}^{s}AL\sigma(i)} \quad \text{(for SM-3 chromosomes)} $$

where:

${}^{1}AL\sigma(i)$ = the absolute length of the long arm of the ith chromosome in a particular male cell.

$\sum_{i=1}^{42} {}^{l}AL\sigma'(i) + \sum_{i=1}^{42} {}^{s}AL\sigma'(i)$ = the total absolute length of the chromosomes in a particular male cell having 42 chromosomes.

${}^{l}RLC\sigma'(i)$ = the relative length of the long arm of the ith chromosome of a male cell on the basis of genome length.

${}^{s}RLG\varphi(i)$ = the relative length of the short arm of the ith chromosome of a female cell on the basis of group length.

Because variation in measurements from cell to cell is a consequence of the coiling cycle of chromosomes, magnification, and photographic enlargement, it is necessary to convert absolute measurements to relative measurements so that inter-nuclear comparisons can be made with a standardized base. It is also advantageous to determine mean values for the arm lengths of specific subgroups on an RLG base. Such means can be calculated as follows:

$$\overline{l}_{RLG\sigma'} = \frac{\sum_{j=1}^{n} {}^{l}RLG\sigma'(j)}{N}$$

where: $\overline{l}_{RLG\sigma'}$ = the mean long arm length (RLG) for N number of male cells in a particular chromosomal group. (The group in question may be stated in subscript.)

$\sum_{j=1}^{n} {}^{l}RLG\sigma'(j)$ = the total lengths (RLG) of long arms of a particular chromosomal group in N number of cells.

The tabulation of arm length data on both RLC and RLG bases can be presented in graphical form. RLC data are presented as a two-dimensional coordinate karyogram. In specific instances, both RLC and RLG data are presented similarly as a partial coordinate karyogram. Coordinate karyograms are constructed by plotting the long and short arm length of individual chromosomes against each other on the X and Y axes, respectively. Chromosomes with similar length characteristics will distribute as clusters of points. Because a probability statement regarding the separability of these clusters cannot be made, it will be stated arbitrarily that "if the clusters are two or more standard deviations apart then the clusters may be considered as representing distinct chromosomal groups." (Ruddle, 1964.) The average values between male and female arm length data have been plotted and a line representing one standard deviation has been drawn to each side of the mean for X and Y values. Both Patau (1960) and Ruddle (1964) pointed out that the coordinate karyogram offers a convenient means of recording and relating karyotypic information. Specifically, the number and relationships of the various chromosomal groups can be readily established. Secondly, standard deviations of coordinate values provide an immediate concept of arm length variation and permit a judgment regarding the degree of separability of the chromosomal groups. Finally, the arm ratio of a chromosomal group can be determined directly from the coordinate karyogram by dividing the long arm RLC by that of the short. Moreover, estimates of arm ratios are facilitated by including arm ratio isopleths which are lines drawn through the coordinate system describing coordinates of equal ratio values. Arm ratio isopleths 1.0, 1.7, 3.0, 7.0 and ∞ have been included in Fig. 4. These particular

isopleths separate median, submedian, subterminal and terminal chromosomal groups as previously defined. Having classified the chromosomes into groups on the basis of arm ratio, subgroups can then be designated on the basis of over-all length. The longest chromosomal group in each arm ratio category is termed 1, the next longest 2, and so on. Thus the longest metacentric chromosome is labeled metacentric-1, or simply, M-1, and so on.

RESULTS

Diploid Counts

One hundred and forty-five mitotic metaphase nuclei were photographed from slides of eleven tadpole madtoms (five females and six males). The range and frequency of chromosome counts are recorded in Table I. The number of nuclei photographed per specimen depended

Table I. Variation in diploid counts of mitotic metaphase chromosomes in Noturus gyrinus.

		Diploid Counts							
Sex	N	36	37	38	39	40	41	42	Total
♀	5	2	3	0	2	24	4	40	75
♂	6	1	0	3	3	12	1	50	70
Total	11	3	3	3	5	36	5	90	145
Percent		2.1	2.1	2.1	3.4	24.8	3.4	62.1	100

primarily on the quality of the smear and the frequency of metaphase cells produced by the specimen during the incubation period. The number of nuclei counted averaged 13 per specimen and ranged from 7 to 25.

Diploid chromosome numbers ranged from 36 to 42. The modal count, representing about two-thirds (62.1%) of the nuclei examined, was 2n = 42. With the exception of some cells which had 2n = 40, all other counts occurred with such low frequency (2.1 and 3.4%) that they were judged to represent ruptured cells. Such hypoloid cells revealed no consistent chromosomal variation.

Although one female had an individual modal count of 2n = 40, non-modal counts of this type were sufficiently numberous (24.8%) to warrant special consideration. Approximately 32% of female counts and 17% of male counts were of this particular non-modal type but no particular pattern of chromosome irregularity existed. Modification in arm number such as might be attributed to centric fusions or telomeric associations were not observed. Therefore, it is assumed that the relatively high frequency of 2n = 40 complements in male and female samples was due to random chromosome loss similar to that noted in other non-modal counts.

General Features of the Karyotype

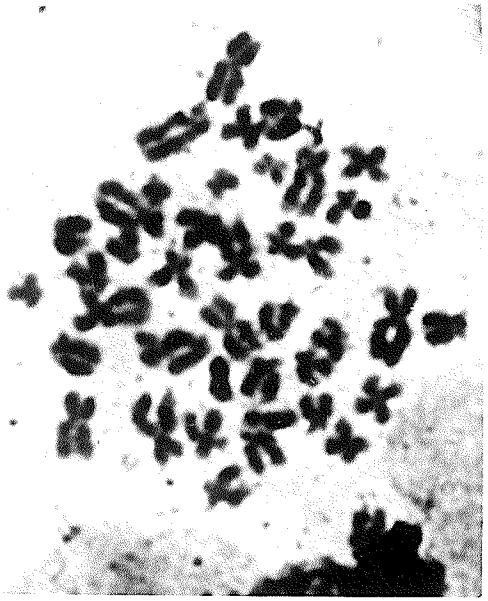
The 42 chromosomes of the tadpole madtom have been divided into nine subgroups on the basis of two karyotypic parameters: over-all chromosome length and arm ratio. These groups are shown in photo-idiograms of female and male cells (Figs. 2 and 3) and as a two dimensional coordinate karyogram (Fig. 4). Three metacentric groups, M-1, M-2, and M-3, can be readily separated by their over-all length. Submetacentric groups, SM-1, SM-2, SM-3, and SM-4, were initially placed together but subsequent analysis (discussed later) indicated that they are distinctive. There are two groups of subtelocentrics, ST-1 and ST-2. Subgroup ST-1 consists of only one pair of large homologs while subgroup ST-2 contains nine pair of smaller homologs.

Because their inherent lengths grade imperceptably into one another, pairing among ST-2 homologs is not meaningful. No telocentric chromosomes are present in the tadpole madtom karyotype.

Mean RLC and arm ratio data for chromosomes from male and female madtoms are tabulated in Table II. Mean values for chromosome arms are specified by subgroup for both male and female samples and the number of chromosomes involved in each average is given. The number of chromosomes in a particular subgroup times the number of cells employed in the study is represented by the number N. The standard deviations from the sample mean as well as the coefficients of variation have been calculated. The V values have been included because they permit variance comparisons between groups that are independent of differences in the magnitude of the group means.

The tadpole madtom karyotype can be characterized in a number of ways using RLC data. First, the mean arm lengths within groups are consistent even for the small number of cells involved. This is supported by the fact that two-way tests of the differences between mean scores for arm length in independently collected samples from males and females are not significantly different at the 5 percent level. The standard deviation for the long arm is on the order of 10 percent of the mean length and 15 percent for the shorter arm. Ruddle (1964) pointed out that increased variance of the short arm measurements as compared to long arm measurements is probably due to experimental error that can be expected to increase as arm length decreases. Imprecision as well as chance distortion of the chromosome will be magnified in the short arm relative to that in the long arm. The data also indicate that the size of the coefficient of variation is a

Figure 2. Photoidiogram of Noturus gyrinus, female.



Noturus gyrinus

(female)

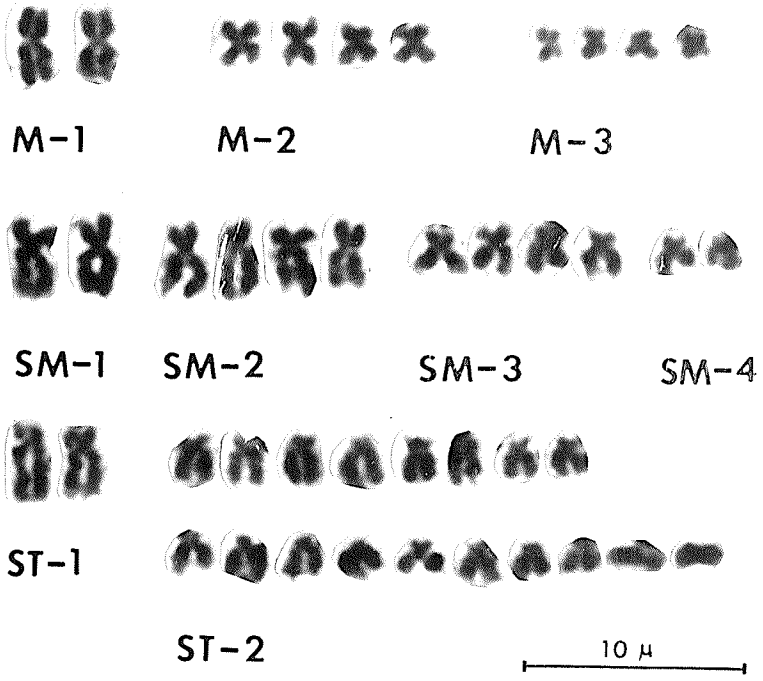
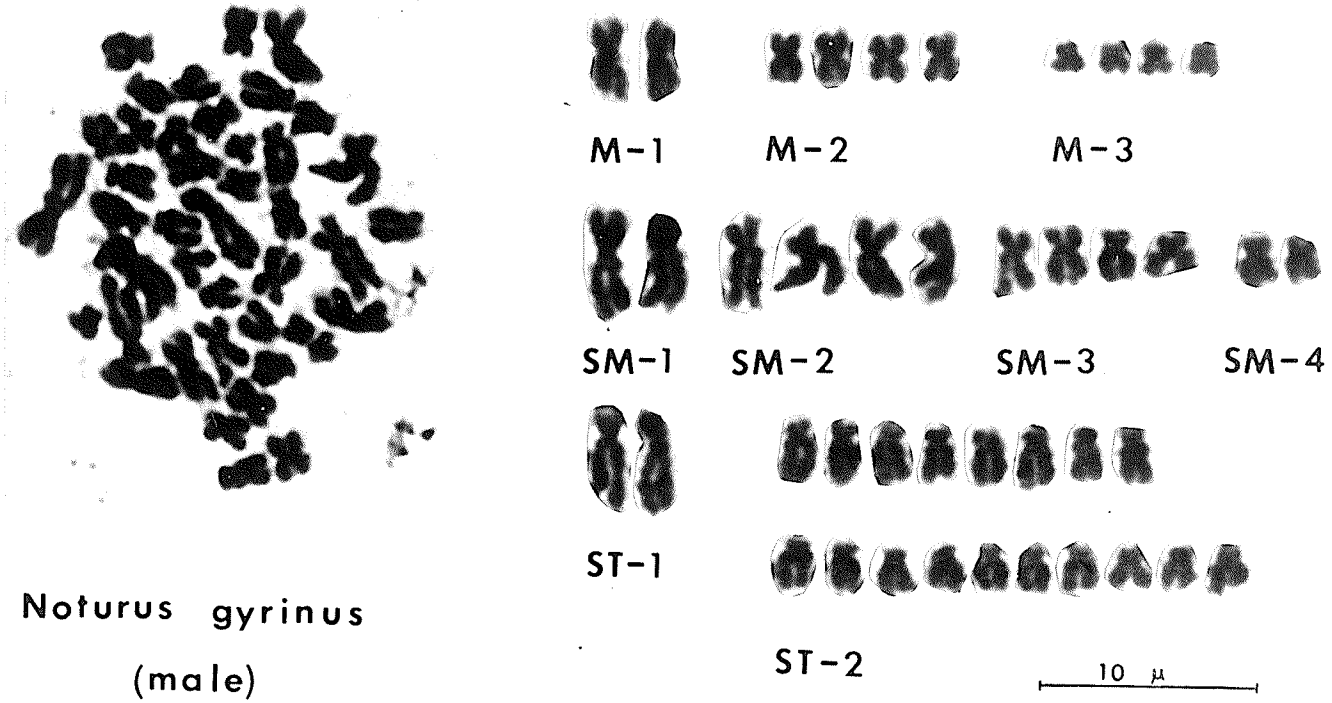


Figure 3. Photoidiogram of Noturus gyrinus, male.



Noturus gyrinus

(male)

Figure 4. Coordinate karyogram of Noturus gyrinus chromosomes, based on arm length averages (RLC).

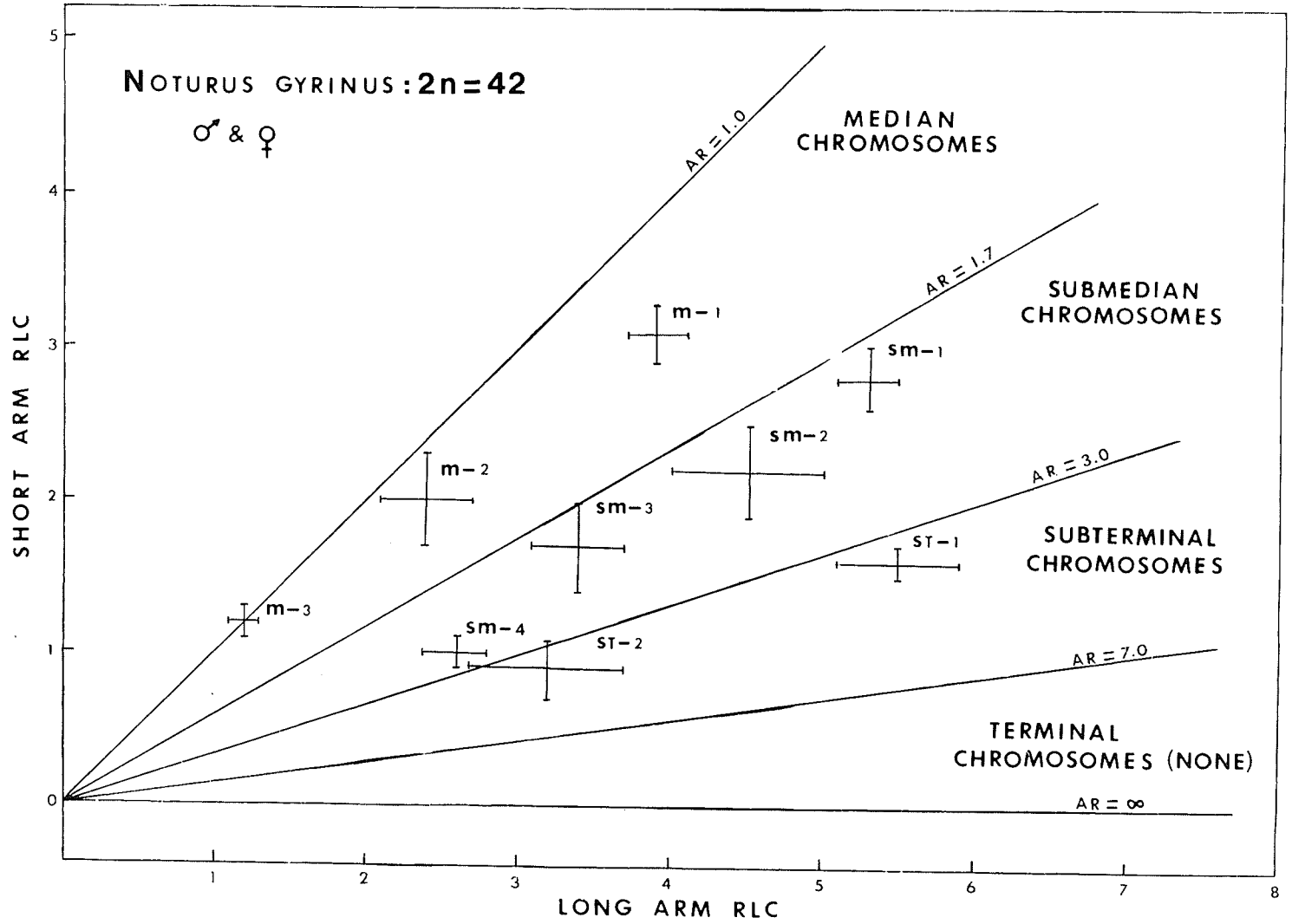

NOTURUS GYRINUS: 2n=42
♂ & ♀
AR = 1.0
AR = 1.7
AR = 3.0
AR = 7.0
AR = ∞
MEDIAN CHROMOSOMES
SUBMEDIAN CHROMOSOMES
SUBTERMINAL CHROMOSOMES
TERMINAL CHROMOSOMES (NONE)
m-1
m-2
m-3
sm-1
sm-2
sm-3
sm-4
ST-1
ST-2
SHORT ARM RLC
LONG ARM RLC
0
1
2
3
4
5
6
7
8

Table II. Arm lengths and arm ratios of chromosomal groups.

			Long Arm			Short Arm			Arm Ratio		
Group	Sex	N	$\overline{RLC}$[a]	s[b]	V[c]	$\overline{RLC}$	s	V	$\overline{AR}$[d]	s	V
M-1	♀	10	4.04	0.16	3.96	3.10	0.18	5.81	1.31	0.04	3.05
M-1	♂	10	3.67	0.24	6.54	3.00	0.18	0.00	1.23	0.08	6.50
M-2	♀	20	2.31	0.35	15.15	1.98	0.33	16.67	1.18	0.13	11.02
M-2	♂	20	2.46	0.23	9.35	1.99	0.30	15.08	1.25	0.15	12.00
M-3	♀	20	1.20	0.06	5.00	1.20	0.06	5.00	1.00	0.00	0.00
M-3	♂	20	1.26	0.03	2.38	1.26	0.03	2.38	1.00	0.00	0.00
SM-1	♀	10	5.34	0.08	1.50	2.78	0.18	6.47	1.93	0.12	6.22
SM-1	♂	10	5.34	0.25	4.68	2.86	0.23	8.04	1.87	0.14	7.49
SM-2	♀	20	4.46	0.55	12.33	2.10	0.23	10.95	2.15	0.40	18.60
SM-2	♂	20	4.63	0.48	10.37	2.30	0.40	17.39	2.19	0.48	21.92
SM-3	♀	20	3.60	0.31	8.61	1.71	0.15	8.82	2.12	0.25	11.79
SM-3	♂	20	3.22	0.36	11.18	1.68	0.36	13.53	1.98	0.22	11.11
SM-4	♀	10	2.52	0.10	4.00	1.06	0.06	5.45	2.44	0.05	2.49
SM-4	♂	10	2.58	0.20	7.69	1.04	0.11	11.00	2.47	0.02	8.10
ST-1	♀	10	5.56	0.24	4.32	1.56	0.16	10.26	3.60	0.48	13.33
ST-1	♂	10	5.50	0.48	8.73	1.66	0.08	4.82	3.31	0.22	6.65
ST-2	♀	90	3.23	0.55	17.03	0.87	0.27	31.03	3.93	0.85	21.63
ST-2	♂	90	3.20	0.50	15.62	0.88	0.22	25.00	3.75	0.72	19.20

a $\overline{RCL}$ = Mean relative length expressed as a percentage of the genome length.
b s = Standard deviation
c V = Coefficient of variation
d $\overline{AR}$ = Mean arm ratio

function of (a) mean arm ratio ($\overline{AR}$) and (b) the number of homologs (N) in the group. For example, the single pair of M-1 homologs has about the same mean total length (7 percent) as a single pair of ST-1 homologs. However, the coefficient of variation for the ST-1 short arm which has a mean arm ratio equal to 3.5 ± 0.8 (Table II) is considerably greater than that of the longer M-1 short arm which has a mean arm ratio equal to 1.3 ± 0.1 Similarly, the size of the V score reflects the number of homologs in the group. Chromosomes in groups M-1, SM-1, SM-4, and ST-1 have only one homolog and give the lowest V scores (about 10 percent). Chromosomes in groups M-2, M-3, SM-2, and SM-3 have three homologs and, with the exception of group M-3, give higher V scores (about 20 percent). Low variability among M-3 chromosomes is probably due to their very small size and near-median centromere. A bias toward perceiving both arms as equal measures combined with imperceptible length variations tends to obscure real differences that undoubtedly exist. Therefore, the arm lengths and arm ratios for M-3 chromosomes are likely more variable than the data suggest. Corresponding differences within groups composed of larger chromosomes, such as group ST-2, are more accurately reflected in their V scores. As previously noted, V scores for long arms in extremely subcentric groups such as ST-2 tend to be lower ($V♀ = 17.03$; $V♂ = 15.62$) than for short arms ($V♀ = 31.03$; $V♂ = 25.00$). No consistent differences between male and female V scores were noted among the 9 subgroups.

Values for mean arm ratios for each group have been calculated directly from absolute arm length data. These values together with standard deviations and coefficients of variation are given in Table III. Because no significant differences in arm length means between male and

Table III. Combined male and female arm length ratios for chromosomal groups.

Group	N	$\overline{AR}$	s[a]	V[b]
M-1	20	1.27	0.06	4.78
M-2	40	1.22	0.14	11.51
M-3	40	1.00	0.0	0.0
SM-1	20	1.90	0.13	6.86
SM-2	40	2.17	0.44	20.26
SM-3	40	2.05	0.24	11.45
SM-4	20	2.46	0.04	5.30
ST-1	20	3.46	0.35	9.99
ST-2	180	3.84	0.78	20.42

a s = standard deviation.

b V = coefficient of variation.

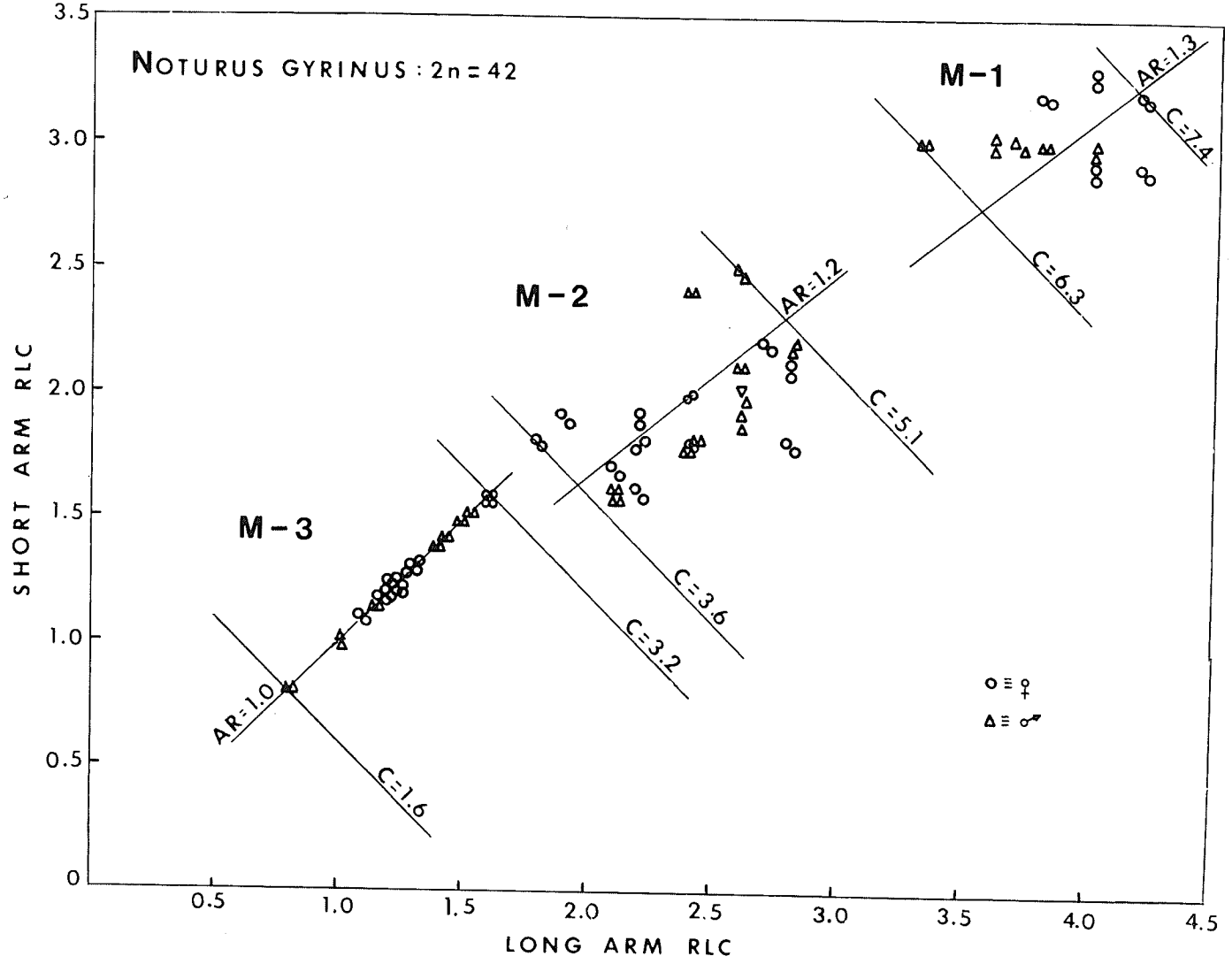
female samples were found, absolute values for both sexes have been combined. The standard deviations again are comparatively low, ranging between 5 and 20 percent of the mean. As in the case of arm length measures, groups with very small, equal-armed chromosomes (M-3) and groups with only one homolog have typically low variability (M-1, SM-1, SM-4, and ST-1). Multiple homolog groups with similar centromeric position in each homolog have somewhat higher scores (M-2 and SM-3). The highest V values are obtained in homogeneous groups in which the arm ratio varies substantially between homologs (SM-2), and in groups with small arms having high experimental error (ST-2).

Median Chromosomal Groups

A partial coordinate karyogram of groups M-1, M-2, and M-3 is shown in Fig. 5. It can be seen that three distinct clusters of points are grouped within the metacentric arm ratio range (1.0-1.7). The clusters are separable not only in terms of over-all length but also on the basis of arm ratio. Arm ratio isopleths have been constructed for each subgroup based on data from Table III. The fit is sufficiently close to a straight line in each group so that it is unnecessary to carry out a regression analysis. These data suggest that the arm ratio for each group is isomorphic over a change of chromosomal length by a factor of 1.2, 1.4, and 2.0 for M-1, M-2, and M-3, respectively. Group M-1 consists of two homologs whose mean arm ratio is 1.27 ± 0.06 (cf. Table III). They are the largest and most asymmetrical metacentrics in the genome. Because M-1 chromosomes have the same over-all length as SM-2 chromosomes (about 7 percent), good preparations are required to achieve arm ratio separation. Group M-2 contains four homologs sufficiently similar in total length (about 5 percent) and arm ratio (1.22 ± 0.14) to make pairing meaningless. In some cells, however, two M-2 homologs were definitely larger than the other two and this variation in over-all length is reflected in V scores on the order of 15 percent (cf. Table II).

So few cells exhibited size differences that consistent pairing within this subgroup would be unreliable without the aid of additional chromosomal markers. Group M-3 consists of the four smallest homologs in the genome and are, therefore, easily classified by inspection. As has been noted, their very small size prevents precise arm ratio descrimination. Hence, distribution of all M-3 chromosomes along the

Figure 5. Partial coordinate karyogram of median chromosomal groups: M-1, M-2, and M-3.


NOTURUS GYRINUS : 2n = 42
M-1
AR=1.3
C=7.4
C=6.3
M-2
AR=1.2
C=5.1
C=3.6
M-3
AR=1.0
C=3.2
C=1.6
○ ≡ ♀
△ ≡ ♂
SHORT ARM RLC
LONG ARM RLC
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5

1.0 RLC arm ratio isopleth probably represents a more perfect fit to this isopleth than is truly the case.

Submedian Chromosomal Groups

The submetacentric chromosomes were most difficult to classify. High variability in absolute length and arm ratio from cell to cell made consistent pairing questionable. Figures 6 and 7 show the same data plotted as RLC and RLG values, respectively.

RLC values (Fig. 7) distributed along the 2.2 mean arm ratio isopleth make descrimination of subgroups inconclusive. Some suggestion of separability of distal homologs from adjacent groups can be seen in the clustering of points at each end of the isopleth. Further evidence of the distinctiveness of the distal clusters is shown in their mean arm ratios which, when calculated separately (cf. Table II), are 1.90 ± 0.13 and 2.46 ± 0.04 for SM-1 and SM-4 chromosomes, respectively. On the other hand, SM-2 and SM-3 homologs have similar arm ratios (2.17 ± 0.44 and 2.05 ± 0.24, respectively) with relatively large standard deviations so that the reality of two distinct sets of homologs can only be demonstrated in terms of total length differences. The partial RLG karyogram (Fig. 7), has an over-all length difference of about 1 percent, separating each of the four sets of homologs. According to convention, "once chromosomal groups have been shown to have little overlap, as in this instance, it is permissible to classify the chromosomes of individual cells into homologs for the purpose of determining mean arm lengths. It should be pointed out that the degree of differentiation that must exist in order to decide whether homologs may be classified with confidence is really undefined." (Ruddle, 1964)

Figure 6. Partial coordinate karyogram of submedian chromosomes.

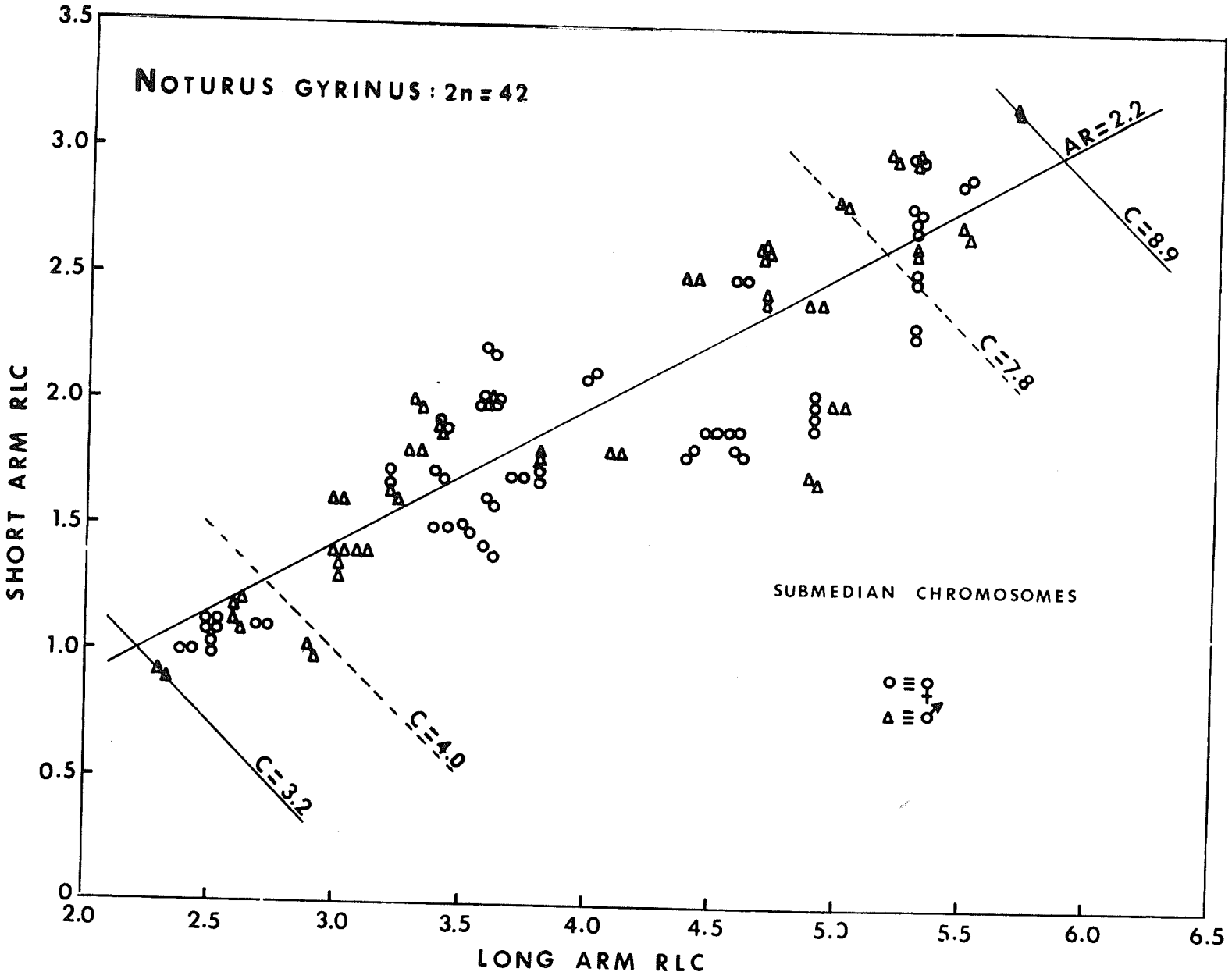
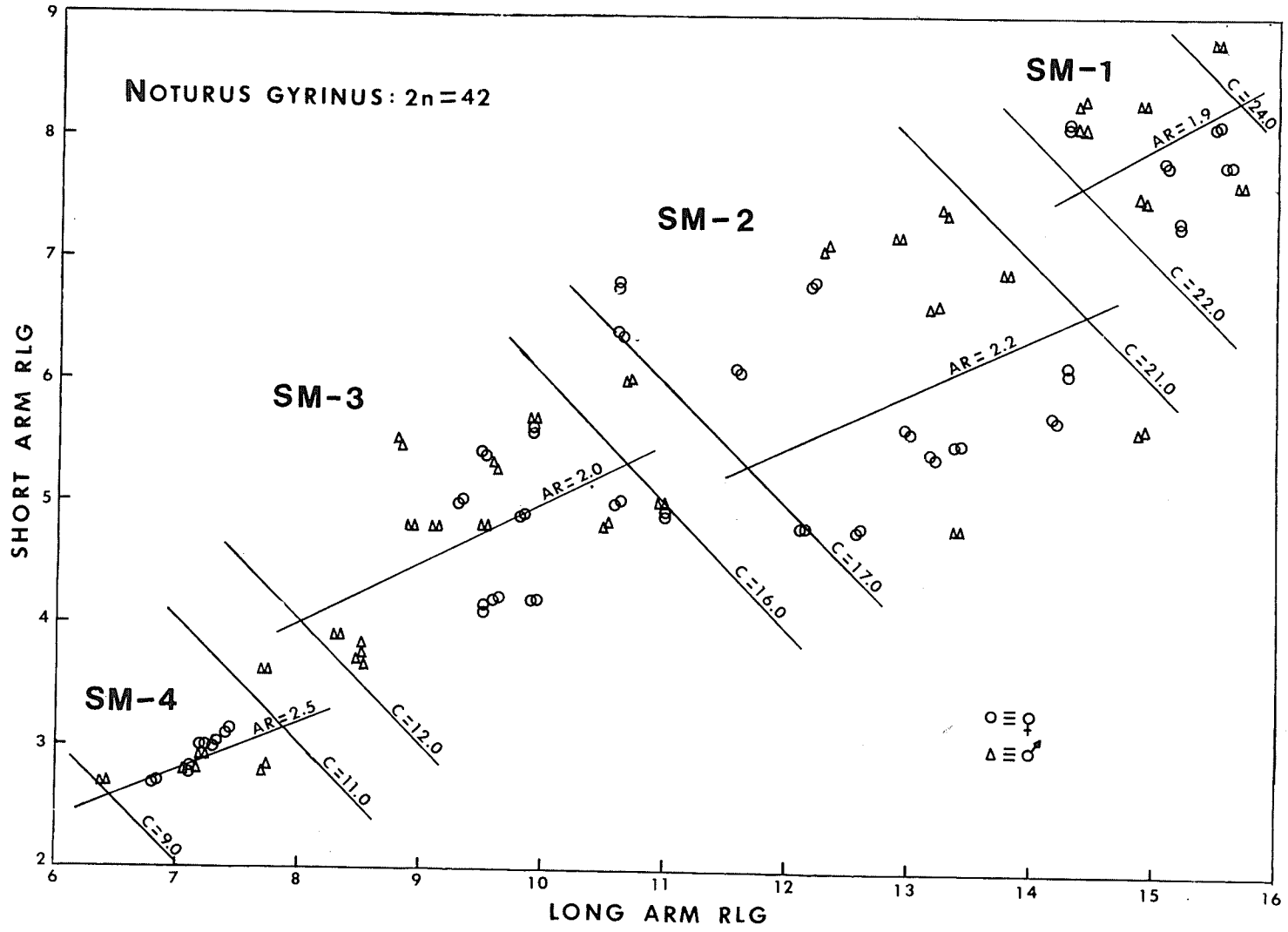

NOTURUS GYRINUS : 2n = 42
AR=2.2
C=8.9
C=7.8
C=4.0
C=3.2
SUBMEDIAN CHROMOSOMES
♀
♂
SHORT ARM RLC
LONG ARM RLC
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5

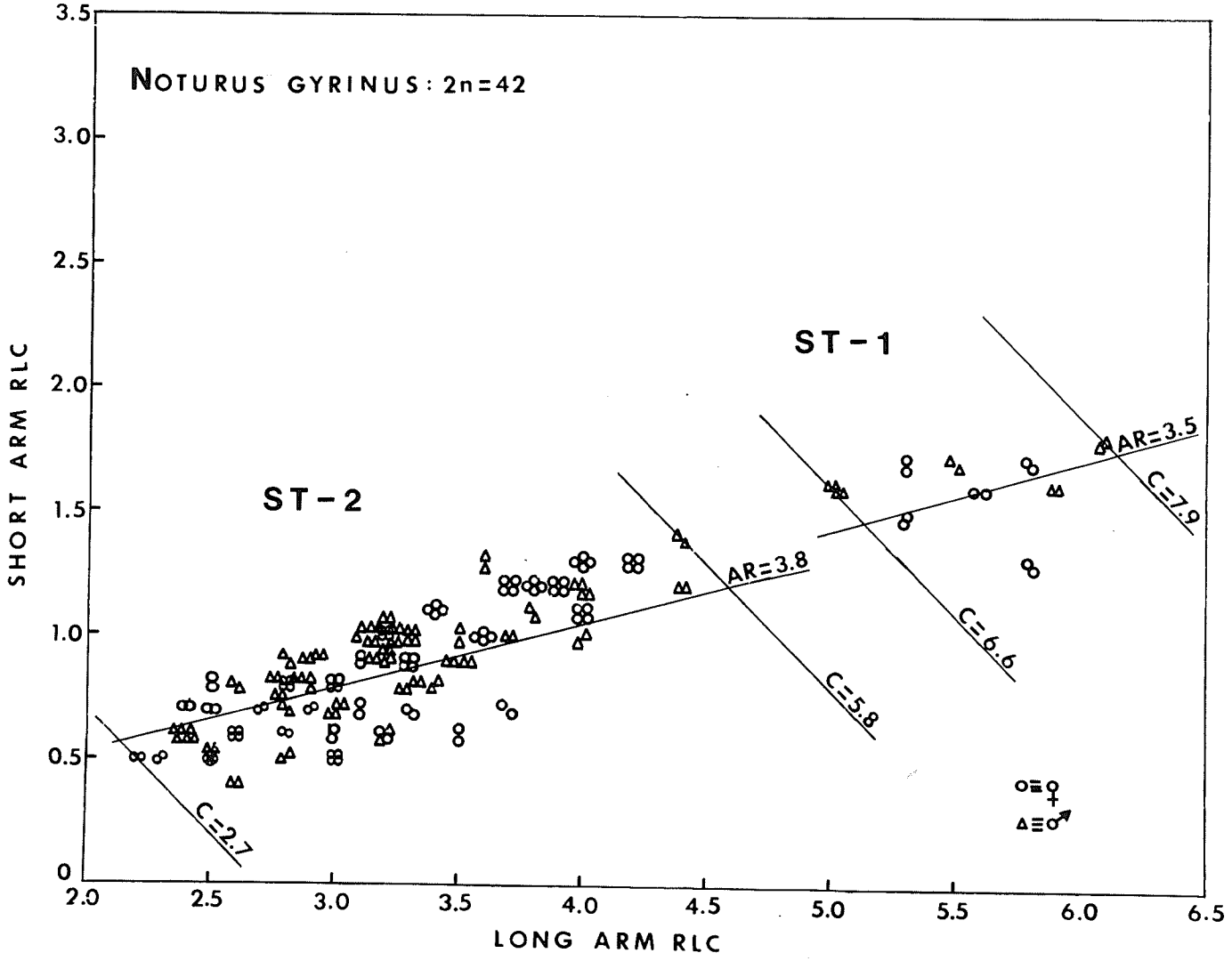
Figure 7. Partial coordinate karyogram of submedian chromosomal groups: SM-1, SM-2, SM-3, and SM-4.


NOTURUS GYRINUS: 2n=42
SM-1
SM-2
SM-3
SM-4
AR=1.9
C=24.0
C=22.0
AR=2.2
C=21.0
C=17.0
AR=2.0
C=16.0
C=12.0
AR=2.5
C=11.0
C=9.0
○ ≡ ♀
△ ≡ ♂
SHORT ARM RLG
LONG ARM RLG
9
8
7
6
5
4
3
2
6
7
8
9
10
11
12
13
14
15
16

Subterminal Chromosomal Groups

The tadpole madtom karyotype contains 20 subterminal chromosomes only two of which are sufficiently different in total length to be paired separately. The remaining 18 subterminal homologs form a continuum for total chromosome length. Figure 8 illustrates the dispersal of subtelocentric chromosomes along mean RLC arm ratio isopleths 3.5 and 3.8 for ST-1 and ST-2 homologs, respectively. ST-1 homologs are readily separated from ST-2 homologs by a genome length factor of about 1 percent and easily distinguished from other large elements, such as M-1, SM-1, and SM-2 chromosomes, by their relatively large mean arm ratio. ST-2 homologs can not be paired on any normalized basis. Partial pairing in some cells can be achieved with satisfaction but there were so few of this type that pairing patterns in ST-2 chromosomes must be regarded as unreproducible. The partial coordinate karyogram (Fig. 8) emphasizes the difficulty of resolving distinct homologous pairs within this group. Because there is no suggestion of discontinuities which might refer to homolog differences, the data were not normalized on an RLG base. Nevertheless, distinctly different chromosomes exist in this population if one considers total chromosome length. The shortest chromosomes have an RLC value of 2.7 while the longest have values of 5.8. When one considers that the standard deviations of mean length (RLC) are on the order of 20 percent of the average length values, length differences between the longest and shortest chromosomes represents a true length difference. Therefore, if only the longest and shortest chromosomes were present, they would be easily separable. Similarly, the arm ratios for ST-2 chromosomes grade from 3.0 to 6.5. Real differences among ST-2 chromosomes do indeed exist but the differences are very slight from one

Figure 8. Partial coordinate karyogram of subterminal chromosomal groups: ST-1 and ST-2.


NOTURUS GYRINUS: 2n=42
ST-1
ST-2
AR=3.5
AR=3.8
C=7.9
C=6.6
C=5.8
C=2.7
♀
♂
SHORT ARM RLC
LONG ARM RLC
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5

set of homologs to another and normal variation tends to obscure them even further. The data suggest that the ability to pair ST-2 homologs on the basis of either arm length or centromeric position is illusory and that these homologs must be considered indeterminate.

DISCUSSION

Muramoto *et al.*(1968) provided evidence that loricarid and ictalurid species are diploid and have acquired varying degrees of genetic redundancy by means of 1) unequal exchange during mitosis, 2) unequal crossing-over during meiosis and 3) regional duplication of chromosomal segments. Consequently, it is supposed that pericentric inversions, divergence of duplicated gene loci and deletion of non-vital chromosomal material has been the primary mechanisms by which modified diploid counts and chromosome structure have evolved from an ancestral siluriform prototype consisting of 50-54 acrocentric chromosomes. (Ohno *et al.*, 1967a.)

While more parametric studies of siluriform karyotypes are needed to elucidate phylogenetic relationships within and between catfish families, comparison of known catfish karyotypes on the basis of apparent chromosome homology can be considered. Chromosome complements of three previously karyotyped catfish together with that of *N. gyrinus* are presented in Fig. 9. Chromosomes of *C. batrachus* are classified according to its investigators. Photoidiograms of *H. plecostomus* and *I. punctatus* are tentatively re-grouped according to over-all length measurements and arm ratio. Initial karyotyping was presumably done by inspection of many nuclei and it is recognized that confident subgrouping would require parametric analysis of more chromosome sets than are immediately available.

Figure 9. Photoidiograms of four catfish species.

A. Clarius batrachus (after Srivastava & Das, 1968), 2n = 52; kf = 6m + 46t.

B. Hypostomus plecostomus (modified from Muramoto et al., 1968). 2n = 54; tentative kf = 10m + 12sm + 14st + 18t.

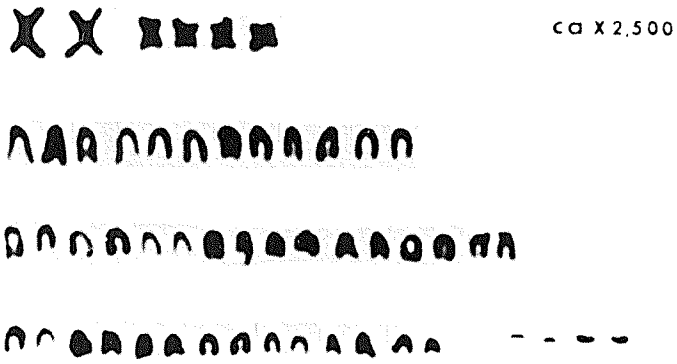
C. Ictalurus punctatus (modified from Muramoto et al., 1968). 2n = 56; tentative kf = 10m + 12sm + 16st + 18t.

D. Noturus gyrinus. 2n = 42, kf = 10m + 12sm + 20st.

* kf = karyotypic formula.

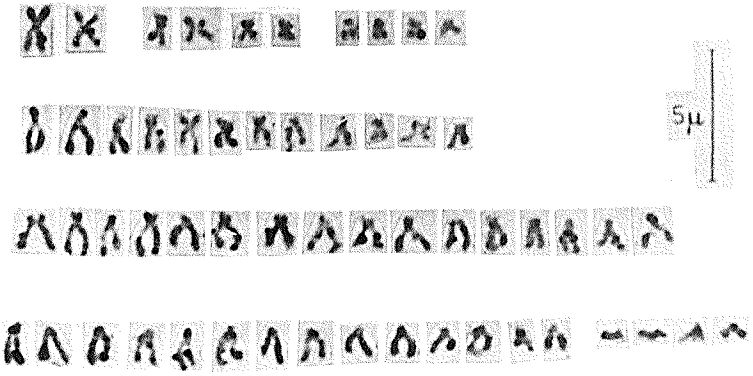
CLARIIDAE

kf Clarius batrachus 2n = 52



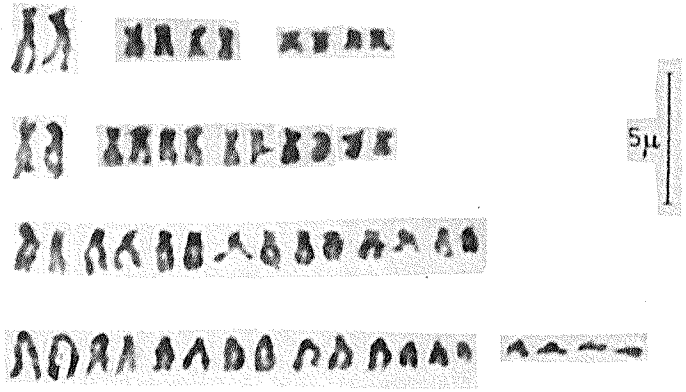
ICTALURIDAE

kf Ictalurus punctatus 2n = 56



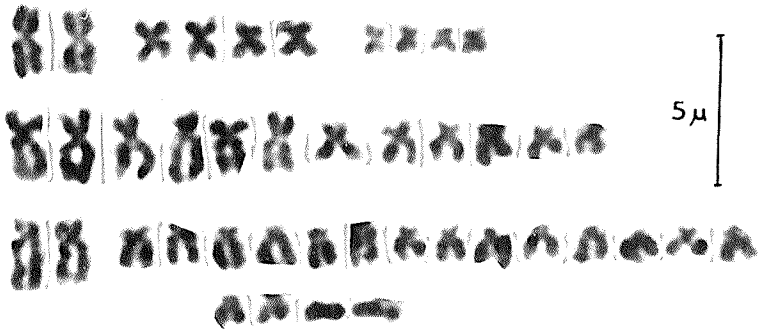
LORICARIDAE

kf Hypostomus plecostomus 2n = 54



ICTALURIDAE

kf Noturus gyrinus 2n = 42



Of the four species available for karyological comparison, C. batrachus appears to have undergone the least chromosomal reorganization. The larger pair of metacentrics and two medium-sized metacentrics are thought to be homologous to M-1 and M-2 groups in N. gyrinus. These six metacentrics probably arose very early in catfish evolution because they appear in representatives of widely divergent siluriform families.

The derivation of two pairs of minute metacentrics (M-3) is obscure. Their presence in both taxonomically primitive and advanced groups, such as Ictaluridae and Loricaridae, and their absence in C. batrachus suggest one of two possibilities. Either an Old World clariid ancestor diverged very early from the main line of catfish evolution, prior to the formation of the M-3 subgroup, or siluriform families of New World origin (tentatively including Ictaluridae) have retained the four M-3 homologs while all or some Old World form have either lost these chromosomes or incorporated them into existing linkage groups. A diploid number of 52 and the presence of 46 telocentrics in the C. batrachus karyotype tends to support the hypothesis that clariid chromosome complements more closely resemble that of the ostariophysian prototype than do other taxonomically primitive and advanced New World catfish groups. Perciform fishes are another example where taxonomically advanced species have retained relatively unmodified chromosome numbers and structure. Thus, it is likely that the ancestral karyotype from which C. batrachus evolved with little structural modification consisted of 52-56 telocentric chromosomes. Nogusa (1960) reports a diploid count of 56 rod-shaped chromosomes for Pelteobagrus nudiceps. This species belongs to Bagridae which is generally regarded as a taxonomically

primitive Old World catfish family.

The chromosomes of H. plecostomus, I. punctatus and N. gyrinus show little morphological resemblance to those of C. batrachus. However, the karyotype of I. punctatus can be equated to that of C. batrachus to the extent that a steady progression of pericentric inversions among 46 telocentrics could provide the 46 submetacentric, subtelocentric and telocentric chromosomes observed in I. punctatus. The inversion process presumably continued further in the Noturus line where, in the case of N. gyrinus, no truly telocentric chromosomes are evident. Seven pairs of telocentrics appear to have either been lost in N. gyrinus or incorporated into existing linkage groups. Whatever the mechanism, considerable genetic consolidation and chromosomal reorganization seem to have accompanied the divergence of Ictalurus and Noturus lines. A similar pattern of chromosomal reorganization and diversification of diploid numbers has been proposed for another group of ostariophysians. According to Ohno et al. (1968) "it appears that an ancestor of the family Cyprinidae [order Cypriniformes] had 48 acrocentrics and a DNA content of about 20% that of mammals. Without substantial change in the DNA content, modification of this karyotype mainly by pericentric inversion subsequently occurred to many members of this family. They came to possess 50 to 54 chromosomes, nearly half of which are metacentric [including submetacentric] ." In the case of siluriform groups, however, Muramoto et al. (1968) point out that "diploid members of Ostariophysi [viz. Siluriformes] underwent extensive chromosomal rearrangement as well as a steady increase in DNA content by regional duplication of chromosomal segments."

It is not possible to deduce the degree of genetic divergence between I. punctatus and H. plecostomus solely on the basis of chromosome morphology. The presence of an additional pair of subtelocentrics accounts for the difference in diploid number between them. Their karyotypes appear to be quite similar in other respects. Spectrodensitometric studies (Muramoto et al., 1968) indicate that the nuclear DNA content of H. plecostomus is 51% that of mammals while that of I. punctatus is only 30%. As a consequence of tandem duplication of DNA segments, it is possible that parametric studies of chromosome length would show the genome length of H. plecostomus to be significantly greater than that of I. punctatus.

SUMMARY

A study has been made of the somatic chromosomes of Noturus gyrinus (Mitchill). The diploid number is 42 and sexual heterogamety was not evident.

Parametric analysis of over-all chromosome length and arm ratio has permitted separation of chromosomes into nine homolog groups. Three median groups consisting of one pair of M-1 homologs, two pair of M-2 homologs and two pair of M-3 homologs have been identified on an RLC base. Separation of four submedian homolog groups was possible only on an RLG base. Submedian groups consisted of one pair of SM-1 homologs, two pair of SM-2 homologs, two pair of SM-3 homologs and one pair of SM-4 homologs. Ten pair of subterminal chromosomes have been identified only one of which (ST-1 homologs) was separable on an RLC base. The remaining eighteen subterminal chromosomes (ST-2 homologs) could not be separated by either base method. Homologous pairing within the ST-2

subgroup was therefore regarded as indeterminate.

Possible derivation of four catfish karyotypes was considered. Clarius batrachus (Clariidae) appeared to have the least modified karyotype consisting of 6 metacentrics (M-1 and M-2 groups) and 46 telocentric chromosomes. The chromosomes of N. gyrinus resembled those of Ictalurus punctatus (Ictaluridae) and Hypostomus plecostomus (Loricaridae) in that all three had 10 metacentric chromosomes (M-1, M-2, M-3 groups) and 12 submetacentric chromosomes (SM-1, SM-2, SM-3, SM-4 groups). The N. gyrinus karyotype contained four more subterminal chromosomes than both H. plecostomus and I. punctatus but was lacking eighteen terminal chromosomes found in the other two species. Hypostomus plecostomus and I. punctatus karyotypes appeared to differ by one subterminal pair of chromosomes. Comparison of homolog groups suggests that the loricarid and ictalurid karyotypes have undergone extensive chromosomal reorganization by means of pericentric inversion while the clariid karyotype appears to have remained relatively unmodified from an ancestral form possessing 52-56 telocentric chromosomes.

APPENDIX

A variety of karyological symbols and nomenclature are used to describe diploid sets of chromosomes. The symbols, as reported by workers cited in the Appendix, are listed and defined below.

Symbol	Karyological description
a	acrocentric chromosomes; subterminal or terminal centromere; rod-shaped chromosomes.
m	metacentric chromosomes; median or near-median centromere; V-shaped chromosomes.
msm	metacentric and submetacentric chromosomes; median or submedian centromere; bi-armed chromosomes.
sm	submetacentric chromosomes; submedian centromere; J-shaped chromosomes.
sn	supernumerary chromosomes; centromere presumed diffuse or lacking; dot-shaped chromosomes.
st	submetacentric chromosomes; submedian centromere; J-shaped chromosomes.
t	telocentric chromosome; terminal or near-terminal centromere; rod-shaped chromosomes.
F	fundamental chromosome; including small metacentric, submetacentric and acrocentric chromosome presumably derived by pericentric inversion.
L	large metacentric or near-metacentric chromosomes presumably derived by centric fusion.
S	satellited F chromosomes.
W	morphologically identifiable female sex chromosomes; female heterogametic.
X	morphologically identifiable female sex chromosomes; female homogametic.
Y	morphologically identifiable male sex chromosomes; male heterogametic.
Z	morphologically identifiable male sex chromosome; male homogametic.
( )	specified sex chromosome not morphologically identifiable.

Annotated chromosome numbers in fish
and fish-like chordates.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Urochordata:							
Ciona intestinalis	28	14		28a, minute	5	testis	Taylor, 1967.
C. intestinalis					6		Atkin & Ohno, 1967.
C. intestinalis	28			28a, minute	6	testis	Ohno et al., 1968.
Styela plicata	32	16		32a	10	testis	Taylor, 1967.
Cephalochordata:							
Branchiostoma belcheri	32	16		32a		testis	Nogusa, 1960.
B. lanceolatum					17		Ohno et al., 1968.
Cyclostomi:							
Eptatretus burgeri	48	24		48a		testis	Nogusa, 1960.
E. okinoseanus	46	23		46a		testis	Nogusa, 1960.
E. stoutii	48	24		48a		testis	Taylor, 1967.
E. stoutii	48			48a, large	78		Ohno, et al., 1968.
Entosphenus reissneri	94-96			94-96a		testis	Nogusa, 1960.
Lampetra planeri	94-96			a, minute	38		Ohno et al., 1968.
Elasmobranchii:							
Dasyatis akajei	84	42		64a + 20m		testis	Nogusa, 1960.
Mustelus manazo	72	36		12m + 60a		testis	Nogusa, 1960.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Teleostei:							
Division I							
Superorder ELOPMORPHA							
Order Anguilliformes							
Suborder Anguilloidei							
Family: Anguillidae							
Anguilla anguilla	38					cornea	Sick *et al.*, 1962.
A. japonica	38					cornea	Sick *et al.*, 1962.
A. rostrata	38					cornea	Sick *et al.*, 1962.
Family: Echelidae							
Echelus uropterus	50	25		46a + 4sm		testis	Nogusa, 1960.
Family: Muraenidae							
Gymnothorax kidako	42	21		30a + 12m		testis	Nogusa, 1960.
Muraena pardalis	40	20		26a + 14m		testis	Nogusa, 1960.
Superorder CLUPEOMORPHA							
Order Clupeiformes							
Suborder Clupeoidei							
Family Clupeidae							
Clupea harengus	52					cell cult.	Roberts, 1966.
C. pallasai	52		60		28	gill, spleen, liver, testis	Ohno *et al.*, 1967b.
C. pallasai	52		60		28	gill, spleen, liver, testis	Klose *et al.*, 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
C. pallasai	52			44a + 6m	28		Ohno et al., 1968.
Hypomesis pretiosus	50±		60		21	gill, liver, spleen, testis	Ohno et al., 1967b.
H. pretiosus	50±		60		21	gill, spleen, liver, testis	Klose et al., 1968.
Sprinchus starksi	50±		60		24	gill, spleen, liver, testis	Ohno et al., 1967b.
S. starksi	50±		60		24	gill, spleen, liver, testis	Klose et al., 1968.
Family Engraulidae							
M. japonicus	48	24		48a		testis	Nogusa, 1960.
Engraulis mordax	48		48		43	gill, spleen, liver, testis	Ohno et al., 1967b.
E. mordax	48		48		44	gill, spleen, liver, testis	Klose et al., 1968.
E. mordax	48		48		40		Ohno et al., 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Division III							
Superorder PROTACANTHOPTERYGII							
Order Salmoniformes							
Suborder Salmonoidei							
Family Salmonidae							
Subfamily Salmoninae							
Onchorhynchus gorbuscha	52					embryo	Simon, 1963.
O. keta	74					embryo	Makino, 1937.
O. keta		50				testis	Nogusa, 1960.
O. keta	74					embryo	Simon, 1963.
O. kisutch	60					embryo	Simon, 1963.
O. kisutch	58-60		104		87	gill, spleen, liver, testis	Ohno et al., 1967b.
O. kisutch	58-60		104		87	gill, spleen, liver, testis	Klose et al., 1968.
O. kisutch	78^{+}_{-}				87		Ohno et al., 1968.
O. masou		50				testis	Nogusa, 1960.
O. nerka		54				testis	Nogusa, 1960.
O. rhodurus		50				testis	Nogusa, 1960.
O. tshawytscha	68					embryo	Simon, 1963.
Salmo alpinus	80			16a		embryo, testis	Svardson, 1942, 1945.
Salmo clarki	64		106	22a + 42m		embryo	Simon & Dollar, 1963

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
S. irideus (=gairdneri)	60						Wright, 1955.
S. irideus	60					embryo	Lieder, 1956.
S. irideus	104	52		90a + 14m		testis	Nogusa, 1960.
S. irideus	60		104	16a + 44m		embryo	Simon & Dollar, 1963.
S. irideus	58-65					embryo, liver, kidney, spleen, testis	Ohno et al., 1965.
S. irideus	59-64				80	spleen, testis	Ohno & Atkin, 1966.
S. irideus	58-64		104		80	gill, spleen, liver, testis	Klose et al., 1968.
S. irideus	58-64		104	36m	80		Ohno et al., 1968.
S. salar	60					embryo	Prokofieva, 1934.
S. salar	60			12a		embryo, testis	Svardson, 1942, 1945
S. salar	56					embryo	Boothroyd, 1957, 1958, 1959.
S. salar	60					embryo	Rees, 1964.
S. salar	54; 55; 56		72			cell. cult.	Roberts, 1970.
S. trutta	84					embryo	Prokofieva, 1934.
S. trutta (=fario)	84					embryo	Pomini, 1939.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
S. trutta	84					embryo	Svardson, 1942.
S. trutta	80			16a		embryo, testis	Svardson, 1945.
S. trutta	80					embryo	Rees, 1964.
S. trutta	77-82		100			gill, spleen, liver, testis	Klose *et al.*, 1968.
S. trutta	80±						Ohno *et al.*, 1968.
Salvelinus fontinalis	80					embryo	Prokofieva, 1934.
S. fontinalis	84			16a		embryo	Svardson, 1945.
S. fontinalis	84					embryo	Wright, 1955.
S. fontinalis		50				testis	Nogusa, 1960.
S. namaycush	84					embryo	Wahl, 1960.
Subfamily Coregoninae							
Coregonus albula	82					embryo, testis	Svardson, 1942.
C. albula	80		96	16a		embryo, testis	Svardson, 1945.
C. artedii	80		106	16m + 10sm + 54a		embryo	Booke, 1968.
C. asperi	ca36						Kupka, 1948.
C. asperi	36				20		Ohno *et al.*, 1968.
C. clupeaformis	80					gill, spleen, liver, testis	Klose *et al.*, 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
C. clupeaformis	80		108	20m + 8sm + 52a		embryo	Booke, 1968.
C. clupeaformis	80						Ohno et al., 1968.
C. exiguus	ca72						Kupka, 1948.
C. exiguus	96						Karbe, 1964.
C. exiguus	80+		100±		90	gill, testis, spleen, liver	Klose et al., 1968.
C. hoyi	80		98	10m + 8sm + 62a		embryo	Booke, 1968.
C. lavaretus	80		96	16a		embryo, testis	Svardson, 1942, 1945.
C. lavaretus	96		96				Karbe, 1964.
C. lavaretus	80		96				Viktorovsky, 1964.
C. lavaretus	ca80				90	gill, spleen, liver, testis	Klose et al., 1968.
C. macrophthalmus					90		Klose et al., 1968.
C. nasus	96		96				Karbe, 1964.
C. oxyrhynchus	96		96				Karbe, 1964.
C. peled	80		92				Viktorovsky, 1964.
C. pidschian	96		96				Karbe, 1964.
C. reighardi	80		104	12m + 12sm + 56a		embryo	Booke, 1968.
C. schinzii	ca72						Kupka, 1948.
C. schinzii	96						Karbe, 1964.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
C. wartmanni	78±3						Bargetzi, 1960.
C. wartmanni	96						Karbe, 1964.
C. wartmanni	ca80						Ohno *et al.*, 1968.
C. zenithicus	80		98	10m + 8sm + 62a		embryo	Booke, 1968.
P. coulteri	82		100	10m + 8sm + 64a		embryo	Booke, 1968.
P. cylindraceum	78		100	12m + 10sm + 56a		embryo	Booke, 1968.
Subfamily Thymallinae							
Thymallus thymallus	102		130	28a		embryo, testis	Svardson, 1945.
T. thymallus					60		Klose *et al.*, 1968.
Family Osmeridae							
Hypomesus pretiosus	52			8m	21		Ohno *et al.*, 1968.
Osmerus eperlanus	58			10m + 48a		embryo, testis	Svardson, 1945.
Suborder Galaxioidei							
Family Salangidae							
Salangichthys microdon		28				testis	Nogusa, 1960.
Suborder Esocoidei							
Family Esocidae							
E. lucius	48					embryo	Prakken *et al.*, 1955.
Family Umbridae							
Umbra limi	22	11				testis	Foley, 1926.
Superorder OSTARIOPHYSI							
Order Cypriniformes							
Suborder Characoidei							
Family Characidae							

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Chalceus macrolepidotus	54			32m + 22st	54	testis, kidney, spleen, gill	Muramoto et al., 1968.
Serrasalmus hollandi	64				48	testis, kidney, spleen, gill	Muramoto et al., 1968.
Suborder Cyprinoidei							
Family Cyprinidae							
Abbottina rivularis	50	25		6m + 44sm		testis	Nogusa, 1960.
Abramis brama	50		80±		36	gill	Wolf et al., 1969.
Acheilognathus cyanostigma	44	22		4m + 40a		testis	Nogusa, 1960.
A. limbata	44	22		4m + 40a		testis	Nogusa, 1960.
A. rhombea	46-48	23-24		2m + 44or46a		testis	Nogusa, 1960.
Barbus barbus	100		144±		49	gill	Wolf et al., 1969.
B. fasciatus	52				22	gill, spleen, testis	Ohno et al., 1967a.
B. semifaciolatus	52	26		4m + 48a		testis	Nogusa, 1960.
B. tetrazona	50			34m	20	gill, spleen, testis	Ohno et al., 1967a.
B. tetrazona	50-52				20-22		Bender & Ohno, 1968.
B. tetrazona	50			34m	20		Ohno et al., 1968.
B. tetrazona	50		90±		20	gill	Wolf et al., 1969.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Carassius auratus	96-104			64m	50	spleen, testis	Ohno & Atkin, 1966.
C. auratus	100			12m + 36sm + 52a		kidney	Ojima et al., 1966.
C. auratus	100			12m + 36sm + 52a		kidney	Ojima & Hitotsumachi, 1967.
C. auratus	≤104				52	gill, spleen, testis	Ohno et al., 1967a.
C. auratus	104				52		Ohno et al., 1968.
C. auratus	≤104		166±		53	gill	Wolf et al., 1969.
C. carpio	≤104				50	gill, spleen, testis	Ohno et al., 1967a.
C. carpio	104			46m + 18st + 36t	50		Ohno et al., 1968.
C. carpio	≤104		168±		52	gill	Wolf et al., 1969.
Ctenopharyngodon idellus	48	24		48a		testis	Nogusa, 1960.
Gnathopogon elongatus	50	25		50a		testis	Nogusa, 1960.
Hemibarbus longirostris	50	25		50a		testis	Nogusa, 1960.
Hemigrammocypris rasborella	48	24		48a		testis	Nogusa, 1960.
Ishikauia steenackeri	48	24		2m + 46a		testis	Nogusa, 1960.
Labeo chrysophekadion	50			14m + 18st + 18a	40	testis, kidney, spleen, gill	Muramoto et al., 1968.
Leuciscus cephalus	50		88±		38	gill	Wolf et al., 1969.
Moroco perenurus		27				testis	Nogusa, 1960.
M. steindachneri	54	27		8m + 46a		testis	Nogusa, 1960.
Opsariichthys uncirostris	66	33		66a		testis	Nogusa, 1960.
Pseudogobio esocinus	52	26		52a		testis	Nogusa, 1960.
Pungtungia herzi	50			4m + 46a		testis	Nogusa, 1960.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Rhodeus ocellatus	44	22		2m + 42a or 4m + 40a		testis	Nogusa, 1960.
Rutilus rutilus	50		78±		28	gill	Wolf *et al*., 1969.
Sarcochielichthys variegatus	50	25		50a		testis	Nogusa, 1960.
Tinca tinca	48		80±		30	gill	Wolf *et al*., 1969.
Zacco platypus	48	24		48a		testis	Nogusa, 1960.
Z. temmincki	50			4m = 46a		testis	Nogusa, 1960.
Family Cobitidae							
Acanthophthalmus khulli	50			14m + 12st+24a	28	testis, kidney, spleen, gill	Muramoto *et al*., 1968.
Barbatula oreas	48			4m + 44a			Makino, 1941.
Botia marcracantha	98			28m + 70a	26	testis, gill, spleen, kidney	Muramoto *et al*., 1968.
Cobitis biwae	54	27		4m + 50a		testis	Nogusa, 1960.
Lefua echigonia	50	25		50a		testis	Nogusa, 1960.
Misgurunus anguillicaudatus	52			52a			Makino, 1941.
Order Siluriformes							
Family Ictaluridae							
Ictalurus punctatus	56			16msm+22st+18a	30	testis, spleen, kidney, gill	Muramoto *et al*., 1968.
Noturus gyrinus	42			10m + 12sm + 20st		gill	Levin, MSc thesis (1972).
Family Bagridae							
Pelteobagrus nudiceps	56	28		56a		testis	Nogusa, 1960.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Family Siluridae							
Parasilurus asotus	58	29		58a		testis	Nogusa, 1960.
Family Clariidae							
Clarius batrachus	52			6m + 46a		kidney	Srivastava & Das, 1968.
Family Loricariidae							
Hypostomus plecostomus	54			24msm+12st+18a	51	testis, gill, spleen, kidney	Muramoto et al., 1968.
Superorder ATHERINOMORPHA							
Order Atheriniformes							
Suborder Cyprinodontoidei							
Family Cyprinodontidae							
Aplocheilus blocki	48	24				testis	Scheel, 1966 b, 1968.
A. dayi	48	24				testis	Scheel, 1966 b, 1968.
A. lineatus	50	25				testis	Scheel, 1966 b, 1968.
A. panchax	36	18				testis	Scheel, 1966 b, 1968.
Aphyosemion arnoldi	36	18				testis	Scheel, 1966 b, 1968.
A. australe	30	15				testis	Scheel, 1966 b, 1968.
A. bertholdi	42	21				testis	Scheel, 1966 b, 1968.
A. bivittatum	40	20				testis	Scheel, 1966 a, 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
A. calliurium	32	16				testis	Scheel, 1966 b, 1968.
A. filamentosum	36	18				testis	Scheel, 1966 b, 1968.
A. guineese	38	19				testis	Scheel, 1966 b, 1968.
A. gulare	32	16				testis	Scheel, 1966 b, 1968.
A. louessense	20	10				testis	Scheel, 1966 b, 1968.
A. nigerianum	36	18				testis	Scheel, 1966 b, 1968.
A. sjoestedti	46	23				testis	Scheel, 1966 b, 1968.
A. spurrelli	26	18				testis	Scheel, 1966 b, 1968.
Cyprinodon variegatus	48	24		2m + 46a		gill, testis	Levin & Foster, unpublished
Epiplatys annulatus	50	25				testis	Scheel, 1966 b, 1968.
E. bifasciatus	40	20				testis	Scheel, 1966 b, 1968.
E. chaperi	50	25				testis	Scheel, 1966 b, 1968.
E. dageti	50	25				testis	Scheel, 1966 b, 1968.
E. fasciolatus	38	19				testis	Scheel, 1966 b, 1968.
E. sexfasciatus	48	24				testis	Scheel, 1966 b, 1968.
E. spilargyreius	34	17				testis	Scheel, 1966 b, 1968

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Fundulus catenatus	46					gill	Setzer, 1968.
F. catenatus	46			2L + 44F		ovarian cult.	Chen, 1971.
F. chrysotus	36						Setzer, 1968.
F. chrysotus	34			14L + 20F (2S + 16A)		ovarian cult.	Chen, 1971
F. cingulatus	46					gill	Setzer, 1968.
F. cingulatus	46		48	2L + 44F (2S + 42A)		ovarian cult.	Chen, 1971.
F. confluentus	48		48	48F(2S + 46A)		ovarian cult.	Chen, 1971.
F. diaphanus	48		52	Xsm; Ym		gill	Chen & Ruddle, 1970.
F. diaphanus	48		52	48F(2S + 42A + 4SM)		ovarian cult.	Chen, 1971.
F. grandis	48					gill	Setzer, 1968.
F. grandis	48		50	48F(4S + 44A)		ovarian cult.	Chen, 1971.
F. heteroclitus	36					embryo	Moenkhaus, 1904.
F. heteroclitus	45					embryo	Pinney, 1918.
F. heteroclitus	48					ovarian cult., gill, kidney, testis, spleen	Chen, 1970.
F. heteroclitus	48		48			ovarian cult.	Chen & Ruddle, 1970.
F. heteroclitus	48		48	48F(2S + 46A)		ovarian cult.	Chen, 1971.
F. kansae	48					gill	Setzer, 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
F. kansae	48		48	48F(2S + 46A)		ovarian cult.	Chen, 1971.
F. lineolatus	46		48	2L+44F(2S+42A)		ovarian cult.	Chen, 1971.
F. luciae	32		52	16L+16F(2S+2SM+12A)		ovarian cult.	Chen, 1971.
F. majalis	48					ovarian cult., gill, kidney, testis, spleen	Chen, 1970.
F. majalis	48		50			ovarian cult.	Chen & Ruddle, 1970.
F. majalis	48		50	48F(2S + 46A)		ovarian cult.	Chen, 1971.
F. notatus	40					gill	Setzer, 1968, 1970.
F. notatus	40		52	8L+32F(2S+26A +2M+2SM)		ovarian cult.	Chen, 1971.
F. notti	46					gill	Setzer, 1968.
F. notti	46		48	2L+44F(2S+42A)		ovarian cult.	Chen, 1971.
F. olivaceus	48					gill	Setzer, 1968, 1970.
F. olivaceus	48		52	48F(2S+44A+2M)		ovarian cult.	Chen, 1971.
F. parvipinnis	48					gill	Setzer, 1968.
F. parvipinnis	48		50	Xsm; (Y)a		spleen	Chen & Ruddle, 1970.
F. parvipinnis	48		48	48F(2S+46A)		ovarian cult.	Chen, 1971.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
F. pulvereus	48		50	48F(4S+44A)		ovarian cult.	Chen, 1971.
F. rathbuni	48		50	48F(2S+44A+2SM)		ovarian cult.	Chen, 1971.
F. sciadieus	44		50	4L+40F(2S+36A +2SM)		ovarian cult.	Chen, 1971.
F. seminolis	48					gill	Setzer, 1968.
F. seminolis	48		48	48F(2S+46A)		ovarian cult.	Chen, 1971.
F. similis	48					gill	Setzer, 1968.
F. similis	48		50	48F(2S+46A)		ovarian cult.	Chen, 1971.
F. stellifer	48			48F			Chen, 1971.
F. waccamensis	48		52	48F(2S+44A+2SM)		ovarian cult.	Chen, 1971.
F. zebrinus	48					gill	Setzer, 1968.
F. zebrinus	48			48F			Chen, 1971.
Garmanella pulchra	48♀			2sm+46a; $2(X_1)_a+2(X_2)_a$		gill, testis	Levin & Foster, 1972.
	47♂	23		1m+2sm+44a; $Ym+(X_1)_a+(X_2)_a$			
Jordanella floridae	48	24		2sm+46a		gill, testis	Levin & Foster, 1972.
Nothobranchius guentheri	38	19				testis	Scheel, 1966 b, 1968.
N. rachovii	18	9				testis	Scheel, 1966 b, 1968.
Pachypanchax playfairi	48	24				testis	Scheel, 1966 b, 1968.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Family Poeciliidae							
Gambusia affinis (=holbrooki)	35-36					testis	Geiser, 1924.
G. affinis	48	24				testis	Roberts, 1965.
Lebistes reticulatus	46						Winge, 1922.
L. reticulatus	46						Vaupel, 1929.
L. reticulatus	46					testis	Iriki, 1932.
Lima dominicensis (=caudofasciata tricolor)	46					testis	Wickbom, 1941.
L. vittata	46					testis	Wickbom, 1941.
Poecilia (=Heterandria) formosa	46					gill	Schultz & Kallman, 1968.
P. (=Poeciliopsis) latidens	48					gill	Schultz, 1967.
P. lucida	48					gill, testis	Schultz, 1961, 1967.
P. (=Mollienisia) sphenops	36					testis	Meyer, 1938.
P. sphenops	46	23				testis	Wickbom, 1941, 1943.
P. sphenops melanistica	38	19				testis	Wickbom, 1941, 1943.
P. sphenops	46					gill	Schultz & Kallman, 1968.
P. occidentalis	48					testis	Schultz, 1961.
P. velifera	46	23				testis	Wickbom, 1941, 1943.
Phalloceros caudimaculatus	46	23				testis	Wickbom, 1941, 1943.
Phallichtys pittieri	46					testis	Wickbom, 1941.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Xiphophorus (=Platypoecilus) couchianus		25				testis	Friedman & Gordon, 1934.
X. helleri	48					testis	Ralston, 1934.
X. helleri		24				testis	Friedman & Gordon, 1934.
X. helleri	48			48a	23	spleen, testis	Ohno & Atkin, 1966.
X. helleri	48			48a	19-23		Ohno et al., 1968.
X. maculatus	48					testis	Ralston, 1934.
X. maculatus		24				testis	Friedman & Gordon, 1934.
X. montezumae		25				testis	Friedman & Gordon, 1934.
X. variatus		24-25				testis	Friedman & Gordon, 1934.
X. xiphidum		25				testis	Friedman & Gordon, 1934.
Suborder Atherinoidei							
Family Atherinidae							
Menidia notata (=menidia)	ca36					embryo	Moenkhaus, 1904.
Superorder ACANTHOPTERYGII							
Order Gasterosteiformes							
Suborder Gasterosteoidei							
Family Gasterosteidae							
Apeltes quadracus	46	23	♂78 ♀77	♂:Wsm; ♀:Wsm,Za		testis, gill, spleen	Chen & Reisman, 1970.
ulaea inconstans	46	23	54			testis, gill, spleen	Chen & Reisman, 1970.

Taxon	Chromosome No. 2n	n	fn	Description	% DNA	Tissues examined	Reference
Gasterosteus aculeatus	42					embryo	Swarup, 1959.
G. aculeatus	42	21	54			testis, gill, spleen	Chen & Reisman, 1970.
G. wheatlandi	42	21	52	♀:(X)a; ♂:Ya		testis, gill, spleen	Chen & Reisman, 1970.
Pungitius pungitius	42					testis	Makino, 1934a, 1934b.
P. pungitius	42	21	70			testis, gill, spleen	Chen & Reisman, 1970.
Order Scorpaeniformes							
Suborder Scorpaenoidei							
Family Synancejidae							
Inimicua japonicus	50	25		50a		testis	Nogusa, 1960.
Suborder Cottoidei							
Family Cottidae							
Cottus bairdii	ca36-38					testis	Hann, 1927.
C. pollux	48	24		48a		testis	Nogusa, 1960.
Order Perciformes							
Suborder Percoidei							
Family Serranidae							
Coreoperca kawamebari	48	24		48a		testis	Nogusa, 1960.
Family Centrarchidae							
Acantharchus pomotis	48					testis	Roberts, 1964.
Ambloplites rupestris	ca48					testis	Baker, 1956.
A. rupestris	48					testis	Roberts, 1964.
Centrarchus macropterus	ca48					testis	Baker, 1956.
C. macropterus	48					testis	Roberts, 1964.
Chaenobryttus gulosus	48					testis	Roberts, 1964.
E. zonatum	48					testis	Roberts, 1964.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Enneacanthus chaetodon	48					testis	Roberts, 1964.
E. gloriosus	48					testis	Roberts, 1964.
E. obesus	48					testis	Roberts, 1964.
Lempomis auritus	48					testis	Roberts, 1964.
L. cyanellus (N.C.)	48					testis	Roberts, 1964.
L. cyanellus (W.Va.)	46					testis cell cult.	Roberts, 1964.
L. cyanellus	46 47 48			2m + 44a 1m + 46a 48a		spleen, testis, kidney	Becak et al., 1966.
L. cyanellus	46-48				31	testis, spleen	Ohno & Atkin, 1966.
L. cyanellus	46-48				30-35		Ohno et al., 1968.
L. gibbosus	48					testis, cell cult.	Roberts, 1964.
L. macrochirus	ca44					testis	Bright, 1940.
L. macrochirus	48					testis	Baker, 1956.
L. macrochirus	48					testis, cell cult.	Roberts, 1964.
L. marginatus	48					testis	Roberts, 1964.
L. megalotis	48					testis	Roberts, 1964.
L. microlophus	48					testis, cell cult.	Roberts, 1964.
Micropterus dolomieui	46					testis, cell cult.	Roberts, 1964.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
M. salmoides	ca48					testis	Baker, 1956.
M. salmoides	46					testis, cell cult.	Roberts, 1964.
Pomoxis annularis	40-50					testis	Baker, 1956.
P. nigromaculatus	48					testis, cell cult.	Roberts, 1964.
Family Sillaginidae							
Sillago sihama	48	24		48a		testis	Nogusa, 1960.
Family Cichlidae							
Symphysodon aequifasciata	60			44m + 16a	35	spleen, testis	Ohno & Atkin, 1966.
S. aequifasciata	60				30-35		Ohno *et al.*, 1968.
Tilapia mossambica	44	22				gill, testis, oogonia	Natarajan & Subrahmanyam, 1968.
Suborder Mugiloidei							
Family Mugilidae							
Cilias pulchella	48	24		48a		testis	Nogusa, 1960.
Suborder Callionymoidei							
Family Callionymidae							
Callionymus richardsoni	38	19		38a		testis	Nogusa, 1960.
Suborder Gobioidei							
Family Gobiidae							

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Acanthogobius flavimanus	44	22		44a		testis	Nogusa, 1960.
Boleophthalmus pectinirostris	46	23		46a		testis	Nogusa, 1960.
Chaenogobius isaza	46	23		46a		testis	Nogusa, 1960.
C. urotaenia	44	22		44a		testis	Nogusa, 1960.
Gobius abei	46	23		46a		testis	Nogusa, 1960.
G. similis	44	22		44a		testis	Nogusa, 1960.
Mogrunda obscura	62	31		62a		testis	Nogusa, 1960.
Periopthalmus cantonensis	46	23		46a		testis	Nogusa, 1960.
Tridentiger obscurus	44	22		44a		testis	Nogusa, 1960.
Suborder Anabantoidei							
Family Anabantidae							
Betta splendens	42						Bennington, 1936.
B. splendens	42			36a		testis	Svardson & Wickbom, 1942.
Macropodus opercularis		21				testis	Svardson & Wickbom, 1942.
Order Pleuronectiformes							
Suborder Pleuronectoidei							
Family Bothidae							
Paralichthys olivaceus	46	23		46a		testis	Nogusa, 1960.
Xystreurys liolepis	48			48a	23	testis, spleen	Ohno & Atkin, 1966.
X. liolepis	48			48a	19-23		Ohno *et al.*, 1968.
Family Pleuronectidae							
Kareius bicoloratus	48	24		48a		testis	Nogusa, 1960.

Taxon	Chromosome No.				% DNA	Tissues examined	Reference
	2n	n	fn	Description			
Limanda yokohamae	48	24		48a		testis	Nogusa, 1960.
Pleuronichthys verticalis	48			48a	19	testis, spleen	Ohno & Atkin, 1966.
P. verticalis	48			48a	19-23		Ohno et al., 1968.
Order Tetradontiformes							
Suborder Balistoidei							
Family Balistidae							
Novodon modestus	40	20		40a		testis	Nogusa, 1960.
Rudarius ercodes	36	18		36a		testis	Nogusa, 1960.
Stephanolepis cirrhifer	34	17		34a		testis	Nogusa, 1960.
Crossopterygii:							
Lepidosiren paradoxa	38				3540	spleen, testis	Ohno & Atkin, 1966.

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